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ECOLOGY OF TWO POPULATIONS OF *Bufo marinus* IN NORTH-EASTERN AUSTRALIA

Thesis submitted by

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for the degree of Doctor of Philosophy
in the Department of Zoology at James Cook University of North Queensland

"Marine toads (*Bufo marinus*) have few admirers and are usually described in a derogatory manner, such as looking like mobile cow patties."

George and Patricia Zug (1979)

Declaration.

I declare that this thesis is my own work and has not been submitted in any other form for another degree or diploma at any University or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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Abstract.

Aspects of the ecology of the terrestrial stage of *Bufo marinus* from two populations in the wet-dry tropics of north-eastern Australia, one at Calvert Hills in the Gulf of Carpentaria of Northern Territory, and the other in the Townsville region on the north coast of Queensland, were examined and compared.

The stages of the toad life cycle examined ranged from small metamorphs, that had only recently emerged from their natal pools, through to large breeding adults. Considerable variation in the growth and survival rates, activity patterns, individual toad size, body condition and shelter requirements were found between and within these two populations.

Once *B. marinus* entered the terrestrial component of its life cycle, ie. emergence onto land at approximately 8mm in length, individual metamorphs were faced with a series of challenges to their survival and growth through to sub-adult size (30mm). The major obstacles to a metamorph's survival through this stage included stresses from dehydration and from high densities of metamorphs present at the water's edge shortly after the peak breeding period in the wet season. Metamorphs remained close to their natal pond until they were large enough to forage without hydric risks. During this time daily survival rate was restricted by environmental factors such as high temperatures. However, metamorph growth rates were dependant on the density of metamorphs, with higher densities reducing the time required to reach juvenile size, ie. approximately 30mm. Once metamorphs obtain this size it appears that they have an increased chance of survival.

Toads above 30mm were subject to a long-term mark-recapture study at Calvert Hills and Townsville. This technique allowed for several aspects of toad population

ecology to be examined including growth rates from sub-adult size and seasonal variations in activity patterns, sex ratio, and body size and condition within a given area alongside a water source.

Growth rates of *B. marinus* were documented from first emergence from water through to adult breeding size. Their rate of growth was shown to be higher than previously reported for the species in endemic areas and other species of *Bufo*. Toads at Calvert Hills grew faster than those at Townsville, and attained adult size within one year. A shorter, hotter wet season, corresponding to the period of highest food availability, accounted for the higher growth rates and increased body condition shown by toad populations at Calvert Hills compared to Townsville populations.

Toad activity patterns were shown to vary according to age, size, and seasonal conditions. When toads first emerge from the water (approximately 8mm) and commence their terrestrial stage their activity was centred at the water's edge. With growth and decreased hydric stresses metamorphs gradually foraged further away from water. The activity of sub-adult and adult toads was influenced by the time since rain periods, such as the wet season. Except for breeding periods, male and female toads generally centred their activity patterns away from water during the wet season especially after recent rain. As time since rain increased, toad activity switched back to the edge of a water source probably as a response to increasing hydric stresses.

The number of toads active at a water source was highest at both locations at the commencement of the dry season thus reflecting the influx of smaller cohorts from wet season breeding activity and the requirement for toads to rehydrate because of the onset of hot, dry conditions. Toad size at a water source was largest during the wet season indicating that larger male and female toads invested more energy into breeding than smaller toads. The number of toads at the water's edge was therefore in favour of males

during all seasons and at both locations. A male-biased sex ratio probably reflected behavioural differences between the sexes rather than actual variation in densities. For instance, during the wet season, females spent considerable time foraging away from water and only came to the water's edge, when gravid, to breed. The presence of some male toads at a water source throughout the breeding season provided them with a selective breeding advantage whenever female toads came to the water to breed.

The body condition of toads declined into the dry season corresponding with low food availability and dehydration stresses. Furthermore, female body condition demonstrated marked variation by increasing rapidly during favourable conditions, but declining after the wet season. This type of variation reflected energy input during the wet season followed by a sharp decline in condition after egg deposition.

Climatic differences explained much of the variation in toad population ecology, such as growth and survival rates, activity patterns and body size and condition, between the two locations. Although both study regions were located within the wet-dry tropics of northern Australia, the dry season at Townsville was less harsh than that experienced at Calvert Hills and was often punctuated with rain periods. In contrast, the length of the wet season at Calvert Hills was shorter and usually consisted of less rain while the dry season was long and characterised by high temperatures. The climatic variation between the two locations led to variations in the length and timing of the breeding season, rate of growth, and survival through the dry season.

The long, hot dry season at Calvert Hills put severe hydric pressures on toads. A critical requirement for toads was therefore the selection of a favourable shelter site, especially during periods of inactivity when nightly temperatures were low. Favourable shelter sites have high relative soil moisture, high temperatures, and the presence of other toads. Favoured shelters are an essential resource especially during the dry season, and

once found by toads, are returned to repeatedly while conditions within the shelter remain favourable and those outside are unfavourable.

Seasonal variation associated with the wet-dry tropics of northern Australia, influences many aspects of *B. marinus* population ecology. Toad populations respond differently to wet and dry seasons by showing breeding or foraging activity during the wet season, and the need to avoid dehydration during the dry season. The seasonal activity patterns of *B. marinus* populations at a water source also affects the structure and size of populations and the growth rates exhibited by toads within those populations.

Finally, two phases of the terrestrial ecology of toad populations in the wet-dry tropics have been identified as being useful for targeting a potential control agent. The first period is the time just after metamorphosis when survival of small toads is restricted by dehydration and high densities. The second period is late in the dry season when toads are active, due to increasing temperatures, but under extreme hydric stress due to the lack of food and increasing temperatures. If developed, the effectiveness of a biological control agent would be highest if implemented during these two phases.

Table of Contents.

Table of Tables.

Table of Figures.

Chapter 1. Introduction and Aims.

The cane toad, *Bufo marinus* (Anura: Bufonidae), is endemic in southern North America, central and northern South America, and on the island of Trinidad (Mungomery 1935; Pippet 1975; Zug and Zug 1979; Easteal 1981), from approximately 27° N latitude (in southern Texas and western Mexico) to 10° S latitude in central Brazil (Zug and Zug 1979). The species occurs in a wide variety of habitats within its natural range, including rainforest and savanna areas, but is more common in lowland (below 1000m in elevation), open areas disturbed by man and in grasslands (Zug and Zug 1979).

B. marinus belongs to a large cosmopolitan family of anurans, the Bufonidae, which contain about 240 species in 18 genera. No representatives from this family occur naturally in Australia (Tyler 1975; Zug and Zug 1979). However, *B. marinus* was introduced into Australia to combat coleopteran sugar cane pests in 1935 and since its introduction the species has successfully colonised large areas, especially within tropical north-east Australia (Freeland 1984).

1.1 Background.

1.1.1 The Introduction of *B. marinus* into Australia.

The history of introductions of *B. marinus* into other countries including Australia is detailed by Easteal (1981). In Australia, as in many other countries, *B. marinus* was introduced as a biological control agent in 1935 to combat two sugar-cane pests, the Grey-backed beetle, *Dermolepida albohirtum*, and the Frenchi beetle, *Lepidiota frenchi* (Covacevich and Archer 1975; Easteal 1981; van Beurden 1981; Freeland 1986b).

1.1.2 History of Australian Introduction.

On June 22, 1935, 101 toads, imported from Hawaiian stock, were introduced into Australia (Tyler 1975; Sabath *et al.* 1981) for breeding and release into sugar cane areas. A few months after their arrival these original toads bred and large numbers of young toads were distributed into sugar cane areas of north Queensland (Mungomery 1936). During the next few years offspring from this original stock were released at several points along the north-east coast of Queensland (Sabath *et al.* 1981).

Although it was claimed that *B. marinus* would have no adverse effect on the Australian fauna (Mungomery 1936) there was opposition to the toad's introduction into Australia (see Froggart 1936; Kinghorn 1938), The primary concerns of naturalists of the time was that *B. marinus* would eat native frogs, and compete for food, shelter and breeding habitats with native amphibians (Freeland 1985).

1.1.3 Subsequent Dispersal and Range Expansion.

By 1941 it was apparent that *B. marinus* was failing to successfully control the two beetle pests (Covacevich and Archer 1975) and that toads had assumed pest proportions (Ormsby 1955). Over the next 50 years the subsequent dispersal and spread of the toad has been well documented (see Covacevich and Archer 1975; van Beurden and Grigg 1980; Floyd *et al.* 1981; Sabath 1981; Sabath *et al.* 1981; Easteal *et al.* 1985; Freeland and Martin 1985; and Seabrook 1991). In many cases the spread of *B. marinus* has been assisted by man (Covacevich and Archer 1975; Freeland and Martin 1985; Seabrook 1991).

1.1.4 Current Range.

The spread of *B. marinus* is continuing rapidly into the Northern Territory, having reached the border during the wet season of 1982/83, Calvert Hills Station in 1985 (W. Freeland; personal communication) and the McArthur River system west of Borroloola during the 1988/89 wet season. The current front of their western distribution is near the Roper River (Alford *et al.* 1995). Other increases in geographical range include northwards into Cape York Peninsula, where Heathlands station reported their first specimen during the 1989/90 wet season (Trevor Mcleod; personal communication), and southwards from northern N.S.W. (Seabrook 1991).

The distribution and range expansion record of *B. marinus* in Australia over the last 60 years has been dramatic. The species has demonstrated marked biological and physiological characteristics in order to adapt to a variety of climatically different habitats (Freeland 1986b; van Beurden 1981). For instance, their success in establishing populations in almost every vegetation zone has been attributed to the toad's adaptability and resilience to temperature and hydric stresses, their high breeding potential (Covacevich and Archer 1975), the availability of a large under exploited food supply and their low rates of predation and parasitism (Freeland 1986b).

Many areas of suitable habitat and conditions for *B. marinus* are yet to be colonised. Using bioclimatic predictions, van Beurden (1981) predicted that *B. marinus* has the potential to occupy much of the eastern coastal seaboard extending well south of their present distribution. In addition, the likelihood of successful introductions and colonizations in the top end of the Northern Territory and north-west Western Australia is high (van Beurden 1981) with colonisation of the northern portion of the Northern Territory by the year 2010 (Freeland and Martin 1985).

1.1.5 Study Background.

B. marinus spread through the Gulf Country of Queensland at about 30 km/year during the early 1980's, and entered the Northern Territory in 1985 (Freeland 1984). As a result of considerable scientific concern of the effects of cane toads on natural ecosystems following this rapid expansion in northern Australia, a large research program was initiated by Dr Bill Freeland late in the 1980's to determine the ecology and opportunities to control cane toad populations. A team of researchers at James Cook University of North Queensland, led by Dr Ross Alford, were provided with funding to undertake such research and since 1986 a series of studies has been undertaken with several aims including:

a. to compare rates of reproduction, growth, and survival of toads between established and recently colonised populations and determine how these respond to the environment;

b. to examine how toads affect native aquatic animals; and

c. to examine patterns of movement by toads and how these respond to environmental conditions.

The research program conducted at James Cook University was conducted in two phases. The goals of the first phase of the study were to document and compare the density, activity patterns, population dynamics and factors controlling toad numbers of the aquatic life stages (by Mark Hearnden), and the terrestrial life stages of *B. marinus* (which forms the basis of this study).

The second phase was conducted to answer several questions that arose from the results of the first phase. These studies included an examination of whether *B. marinus*

eggs and larvae adversely affect freshwater communities (M. Crossland), an investigation into the local and long-distance movements of *B. marinus* and their use of shelter sites by (L. Schwarzkopf and R. Alford), and a more detailed study of the growth and survival of postmetamorphic toads in response to changes in the availability of food and moisture (D. James).

The study on movement patterns of toads evolved from this study after large numbers of toads were captured on successive nights at the same site but only very small numbers were recaptured thus indicating that around watercourses *B. marinus* were extremely mobile. Furthermore, the investigation into shelter use in the field by *B. marinus* was conducted in response to the shelter experiment reported in this study (Chapter 7).

In this study population dynamics of the terrestrial stage of *B. marinus* are examined in two regions; the north-east coast of Queensland and the Gulf Country of the Northern Territory. The population in the north-east coast of Queensland was situated in and around the Townsville region, where toads have been present since 1937 (Freeland 1986a). The population studied in the Gulf Country of the Northern Territory were situated on a property called Calvert Hills. Toads have colonised this location as recently as 1985 (Hearnden 1991). Although both locations are situated in the wet-dry tropics of northern Australia, important climate differences exists between them and are displayed and discussed in Chapter 2.

1.2 *Bufo marinus* as a Pest Species.

The colonising success of *B. marinus* has led to suggestions that its presence in Australian environments poses serious threats to many native species of animals (Freeland 1985). These effects on Australian native vertebrates are well researched and reviewed in Covacevich and Archer (1975) and van Beurden (1978). Since these effects have been documented it has been suggested that biocontrol of *B. marinus* may reduce these threats. Although not entirely the scope of this study, this thesis forms part of a major project to investigate possible measures to control *B. marinus* numbers in Australia. This study therefore aims to provide a greater insight into the ecology of the terrestrial stage of *B. marinus* the results of which may assist in the construction of population models of the life history stages of *B. marinus* that might be most profitably attacked using biological control agents.

To investigate possible effects and methods to control toad numbers in Australian habitats, a thorough understanding of the ecology of the toad is essential. Although *B. marinus* has successfully colonised habitats in Australia for nearly 60 years, and despite their obvious presence in colonised habitats, little is currently known on the population biology of the terrestrial stage of the life history of *B. marinus*. Most of the preliminary work performed on the population biology of *B. marinus* has been reported from within their natural range by Zug and Zug (1979). However, their study concluded that their synthesis on the natural history of *B. marinus* left many inadequacies and encouraged further study into the ecology of the animal. Some of the recognised inadequacies identified from the Zug and Zug (1979) study, such as growth rates of smaller toads, population size and structure over time, and their activity in relation to hydric and shelter requirements, have been addressed in this thesis which reports the results of a long-term study on the population biology of *B. marinus* in northern Australia.

1.3 Classification Used in this Study.

To accurately study the population dynamics of a species with a complex life cycle, it is necessary to know rates of growth and survival during each life-history stage. To examine the dynamics of *B. marinus* populations, information on growth and survival rates immediately after metamorphosis is required. In this study the period between metamorphosis and first reproduction is divided into the metamorph (<30mm snout-vent length, SVL) (Chapter 3), and post-metamorphic stage (≥30mm). The post-metamorphic stage is further divided into juvenile (30-59mm SVL), sub-adult (60-89mm SVL) and adult (≥90mm SVL) stages (Chapters 4 to 6). These size limited stages follow those of Freeland and Kerin (1991). At 30 mm SVL, the rapid changes in morphology and markings that follow metamorphosis (described in Chapter 3) cease. Above 89mm, secondary sex characters are usually well developed (section 4.2.2). This size limit is, however, arbitrary as some toads may attain sexual maturity at sizes as low as 60mm SVL (D. Barton; personal communication).

1.4 First Emergence onto Land.

A single adult female *B. marinus* can deposit large numbers of eggs in one clutch with the number produced varying from an upper limit of up to 50,000 (van Beurden 1980; Freeland 1986b) to a range between 7,000-36,000 (Straughan 1966; Tyler 1975; Hearnden 1991). Small (10-25mm), black or dark brown, round-bodied tadpoles emerge from the jelly surrounding the eggs within 36 hours to 4 days, and require approximately 21-60 days to develop and complete metamorphosis depending on varying environmental conditions (Straughan 1966; Pippett 1975; Zug and Zug 1979; Hearnden 1991). As these stages in the life cycle of *B. marinus* were comprehensively studied by Hearnden (1991) they were therefore not included in this study.

Little information exists on the population dynamics of *B. marinus* immediately after metamorphosis. The first phase of this study (Chapter 3), therefore investigates the density, activity patterns, growth and survival rates of *B. marinus* immediately after large congregations of tadpoles metamorphose at the same time and at a similar size (approximately 8mm in length) and first emerge onto land.

Once on land *B. marinus* metamorphs collectively face a series of new challenges for survival and growth. For instance, the terrestrial environment provides toads with a greater opportunity for growth, by the exploitation of new and varied food supplies, but increases the risk of mortality from environmental factors (Zug and Zug 1979; James 1994). The ideal time for metamorphosis of *B. marinus* is at the beginning of the wet season, corresponding with increasing insect abundance, (and presumably food), and high humidity (Zug and Zug 1979). The likelihood of death immediately following metamorphosis however, is extremely high, being greater than 50% during the first 2 months (van Beurden 1980). From their first emergence onto land at approximately 8mm, until they attain a size of at least 25mm, metamorphs are most vulnerable to predation from terrestrial predators, including adult toads, due to their small size and relatively low toxicity (Zug and Zug 1979; James 1994).

Small toads are also subject to various stresses from competition (ie. high metamorph densities competing for the same food and shelter resources) and the environment (ie. increasing risk of dehydration caused by dry periods, and starvation from lack of food supplies) (Zug and Zug 1979; Freeland and Kerin 1991; James 1994). Mortality risk from predation and from environmental extremes decrease with increasing body size, especially if early growth stages coincide with favourable conditions at the start of the wet season (Zug and Zug 1979). To survive harsh environmental conditions and maximize food supplies, metamorphs vary their behaviour and activity patterns. For

instance, activity has been shown to be influenced and restricted by vegetation cover, substrate moisture and density (James 1994).

Metamorph growth, resulting in morphological changes, also leads to a change in activity patterns (Freeland and Kerin 1991). Furthermore, metamorph growth rates influence juvenile recruitment, but data on metamorph growth of *B. marinus* are sparse. Several studies have suggested that growth of this size class is rapid (van Beurden 1978; Zug and Zug 1979), but none have provided quantitative data on their actual growth rates. Zug and Zug (1979) made an assumption that post-metamorphic growth was at a constant rate of 0.37mm/day while James (1994) demonstrated that growth rate increased in the presence of vegetation and moisture and decreased with higher metamorph densities. Furthermore, James (1994) also showed that metamorph density had no effect on survival but slowed growth.

In summary, very little is currently known on how biotic and abiotic factors affect rates of growth and survival and activity patterns of *B. marinus* populations in northern Australia. Chapter 3 of this thesis provides the first comprehensive study on the population biology of *B. marinus* metamorphs by examining growth and survival over the first 18 days of terrestrial life at various densities. Correlations between the variation in the abiotic environment and metamorph growth and survival are also examined. Furthermore, the density, activity patterns and size-specific movements of *B. marinus* metamorphs are investigated.

1.5 Post-metamorphic Growth.

Once toads survive through to approximately 30mm SVL their rapid growth rates are believed to be one of the main reasons why they have successfully colonised numerous

habitats (Freeland and Kerin 1988). This growth has been previously identified as highest during the sub-adult stages (between 30 and 89mm SVL) and slows once adult size (≥90mm SVL) has been achieved (Zug and Zug 1979). Growth rates of anurans however, are rarely constant throughout different climatic periods but are usually seasonal and depend on their activity and food supplies. For example, the highest rates of growth reported for *B. marinus* occur at the peak of food abundance during the early wet season (Zug and Zug 1979). Conversely, low growth corresponds with reduced food abundance during the end of the wet and during the entire dry season (Zug and Zug 1979; van Beurden 1980).

No data on growth rates of *B. marinus* populations in the wet-dry tropics of northern Australia currently exists. Chapter 4 of this study therefore aims to document the growth rates of post-metamorphic toads at two climatically different locations by presenting and analysing the results of a long-term mark-recapture study. Recaptured toads provide information on seasonal changes in growth and growth curves can therefore be generated from such data.

The only growth curve documented for *B. marinus* is from populations in their native range (see Zug and Zug 1979), and shows a rapid increase to adult size within the toad's first year since metamorphosis. Growth then slows reaching an asymptotic length of approximately 120mm after three years. Once having attained a size of 110mm most toads demonstrated slower growth rates with some larger toads exhibiting little or no growth (Zug and Zug 1979).

Growth curves can also provide information on the time required for toad populations to reach sexual maturity and this time has been reported to vary. Straughan (1966) and van Beurden (1978) suggested that sexual maturity is attained when toads are two years old, while Zug and Zug (1979) stated that a one-year old individual may be

sexually mature, but would contribute little towards reproduction until its second year. Zug and Zug (1979) hypothesised that older toads would out compete younger, smaller toads and therefore have a higher breeding potential and input into the population. However, as some Australian individual toads may be sexually mature at sizes as low as 65mm snout-vent length (Alford *et al.* 1995), and have gametes present all year round (Hearnden 1991), growth curves of Australian toads may show that they could breed within a year.

1.6 Population Structure.

The structure of Anuran populations has been given much attention over the years. Seasonal changes in activity, body size and condition provide important ecological data of a toad population by identifying areas where they are both most and least successful. The investigation of these ecological aspects of *B. marinus* populations in northern Australia will therefore provide valuable base-line data on toads which may be ultimately used to help control their populations. Chapters 5 and 6 of this thesis report on variation in the seasonal activity of *B. marinus* populations and subsequent changes in their body size and condition.

The primary method used to determine seasonal changes in activity, body size and condition of toads during this study was by a long-term mark-recapture census of two populations in northern Australia. This method best represents the active proportion of a toad population within a given area around a water source (Hearnden 1991).

1.6.1 Toad Activity.

The number of male, female and sub-adult and juvenile toads active around a water source on a particular night will depend on many factors including environmental conditions, such as temperature and rainfall, food availability and breeding activity. Van Beurden (1980), for example, showed that toad activity was positively correlated with percentage of cleared habitat and the amount of available fresh water, while Zug and Zug (1979) suggested that toads were concentrated around ponds because of a higher available food supply and found densities away from water as low as one toad per hectare compared to approximately 80 toads per hectare around water sources. Toads have been shown to make periodic and consistent movements to water holes (Carpenter and Gillingham 1987) and high levels of activity could probably not be sustained without such a water source.

As Anuran activity is primarily dependant on temperature, humidity and precipitation it usually varies between climatic regions. For example, in sub-tropical regions (eg. northern N.S.W.), the emergence of a toad from a refuge and nightly activity was significantly influenced by temperature, with moisture factors being less important as free water is readily available (van Beurden 1979). In tropical areas however, nightly activity of *B. marinus* increases with rainfall (Carpenter and Gillingham 1987).

Periods of inactivity usually exceed periods of activity (Zug *et al.* 1975; Zug and Zug 1979) with only between 30-50% of the total population active even during the most favourable conditions (Zug and Zug 1979). Furthermore, except for the small metamorph stages, *B. marinus* activity is predominately nocturnal. Individual activity at night however, can vary considerably. Toads are seldom active all night but usually show greatest feeding activity 1-2 hours after dusk, when temperatures are highest, a pattern typical of nocturnal ectotherms (Zug and Zug 1979).

In addition to feeding and breeding behaviour, the activity and movement behaviour of *B. marinus* is probably also a mechanism to reduce water loss, with local movement in response to water availability (Carpenter and Gillingham 1987). *B. marinus* activity is usually described as movement within an activity centre, often contained within an area a considerable distance away from a water course, and is highest during the wet season, being stimulated by rain (Zug and Zug 1979), and depressed in the dry season (Zug *et al.* 1975; Carpenter and Gillingham 1987; Schwarzkopf and Alford 1996). Brattstrom (1962) reported a three day activity cycle in the middle of the wet season. However, consecutive dry days within a wet season may reduce toad activity (Zug and Zug 1979).

In North Queensland, *B. marinus* have been shown to exhibit three types of seasonal-dependant movement patterns including short-term localised movements, long treks and longer linear treks (Schwarzkopf and Alford, in press). During the dry season active toads make consistent and periodic movements from their activity centres to a waterhole for rehydration, while during periods of rain, toads forgo their waterhole visits and are able to rehydrate within their activity centre (Carpenter and Gillingham 1987). During the wet season the requirement for close contact with water is not as high, and toad activity correlates with increases in humidity and prey abundance (Zug and Zug 1979). Toads probably take full advantage of blooms of insects and arthropods which often occur at the start of the wet season (Janzen 1973; Freeland and Kerin 1988), by maximising feeding efforts, growing rapidly, and laying energy stores for breeding or survival during leaner periods of wet and dry seasons (Zug and Zug 1979). Low activity in the dry season probably reflects hydric pressures due to the aridity of the air and soil (Zug and Zug 1979), and low prey abundance. The abundance of some tropical insects and other arthropods are low during the mid to late dry season (Freeland *et al.* 1986a).

Activity patterns also vary between the sexes. Several studies have suggested that female toads spend more time away from water than males (Straughan 1966; van Beurden

1978; 1979; Hearnden 1991; Schwarzkopf and Alford 1996), and are more active than either males and sub-adults (Zug and Zug 1979). Hearnden (1991) suggested that, provided conditions were not too dry, only gravid females would enter a breeding site to reproduce and after reproduction would remain outside these areas for the duration of the breeding season. Male movements, on the other hand, are concentrated around a calling site, whereas females kept well away from and were not associated with calling sites (Schwarzkopf and Alford, in press).

1.6.2 Sex Ratios.

Seasonal activity of toads can lead to observable changes in the sex ratio of a toad population during a mark-recapture census. For example, lower male to female ratios at water sources during the late dry season, compared to those recorded during the wet season, may be a result of reduced male numbers in comparison to females and is linked to non-active males remaining within their shelter sites (Hearnden 1991).

In most species of the genus *Bufo*, male toads usually outnumber females at water sources. The difference in sex ratios varies for populations in different habitats (van Beurden 1979; Zug and Zug 1979) and is determined by environmental and biotic conditions encountered by each population (Zug and Zug 1979). During the breeding season toad populations may consist of predominately males (male-biased sex ratio of 10:1), but this ratio declines as activity decreases into the dry season and the sex ratio approaches 1:1 (Hearnden 1991). Van Beurden (1978; 1979) suggested that the actual sex ratio of toad populations was 1:1 and that a male-biased sex ratio was due to males being seen more often than females due to behavioural and activity differences between the sexes. A highly skewed sex ratio therefore depends on the proximity of collecting area to

spawning sites as males were more often in breeding areas than females (van Beurden 1979).

1.6.3 Seasonal Changes in Individual Size.

One main reason for the success of *B. marinus* is that their large size (100-150mm), when compared to other anurans, decreases the probability of predator attacks (Zug and Zug 1979). Large body size also provides toads with a favourable surface to volume ratio thus reducing the relative rate of desiccation (Krakauer 1970).

Habitat and the number of toads active within an area can influence the size reached by adult toads (Pippett 1975). For example, as the number of toads active within a certain area increases the size of the individual toad decreases (Alcala 1957). *B. marinus* populations in closed forests have been shown to have lower number of toads active and therefore usually exhibit larger individual size than those in savanna areas with higher numbers active (Zug and Zug 1979). It has not been determined however, if this variation in individual body size is a function of population density or an effect of climate.

The body size of toads may also vary between localities with similar habitat types. Freeland *et al.* (1986b) presented data showing that Townsville toads exhibited poor body condition and small body size when compared to toad populations in the Gulf of Carpentaria near Calvert Hills. This decrease in body size was despite lower numbers of toads active, higher food intake and lower rates of parasitism compared to Gulf of Carpentaria populations (Freeland *et al.* 1986b; Freeland 1986a). These differences are most likely due to climatic differences between the two locations and the implications of these differences are further discussed in Chapters 4 to 6.

Females of many anuran species reach larger body sizes than males and *B. marinus* is no exception. Larger female size probably increases their reproductive potential by enabling them to carry more eggs (Zug and Zug 1979). Van Beurden (1980) showed that in sub-tropical areas female toads grew for longer periods and showed a faster growth rate than males. This result is possibly due to the greater amount of time females spend foraging, whereas males reduce feeding during periods of breeding activity (van Beurden 1980). Although male toads do not obtain the large sizes shown by females some breeding advantages in larger size have been shown. For example, male-male competition during breeding in *B. marinus* can result in the displacement of smaller males, with resultant amplexing males significantly larger than non-amplexing males (Hearnden 1991).

1.7 Body Condition.

The body condition of toads, measured as a function of their weight to length (see Chapter 6) provides an insight into the relative health of a toad population. In Australian toad populations, the body condition of *B. marinus* has been shown to vary according to season and sex with variation being most pronounced among sub-adults (van Beurden 1980). However, in populations within the toad's natural range no apparent difference in the length/weight relationship occurred between regions (Zug and Zug 1979).

A regression of log body weight by log length used on *B. marinus* by van Beurden (1978) found that, although there was considerable geographic variation, toad body condition was cyclic, with the lowest condition corresponded with minimum activity, and highest condition was attained just before breeding activity. Female toads may require a period of intense feeding to replenish their lipid stores before reproduction and, together with males, store fat bodies for periods of non-breeding corresponding to the dry season (Zug and Zug 1979).

An overall decline in the body condition of *B. marinus* populations in Australia is believed to be consistent with an eruptive population phase peaking at about 8-10 years since colonisation, followed by a food-limited decline (van Beurden 1979). This decline has been noted by other researchers (Alcala 1957; Pippett 1975; Freeland 1986a; 1986b; Freeland *et al.* 1986a). Freeland (1986b) suggested that toad populations undergo an initial post-introduction period of rapid growth, remain relatively stable at high densities for an extended time and then decline in association with reduction in body size and condition. However, he demonstrated that a limited food supply, the number of fat bodies and rates of parasitism are not responsible for the decline, but proposed that it may be due to the presence of an unidentified microbe.

The decline in toad body condition during the dry season in the wet-dry tropics of northern Australia may simply reflect the depletion of energy reserves as a result of severe dry conditions and the lack of adequate food supplies. A higher body condition at the end of the wet season may therefore increase an individual toad's chances of survival through the dry season to the following wet season. Chapter 6 examines the changes in toad body condition between two locations in the wet-dry tropics of northern Australia where minor seasonal climatic variations may reflect these changes.

1.8 Shelter Requirements.

The temperature and/or water economy of toads may influence their geographical distribution, habitat selection and activity patterns. Dehydration stress is lessened by large body size and the presence of a water reservoir in the form of a bladder (Walker and Whitford 1970). An increased size to volume ratio provides toads, as with most amphibians, with the ability to survive longer in a dehydrating environment (Krakauer 1970).

The body temperature of toads is closely linked with ambient temperature (Zug and Zug 1979). High temperatures in the wet-dry tropics of northern Australia therefore place considerable stresses on the water economy of toads. The quality and quantity of shelter or retreat sites are probably essential for toad survival through the dry season to the following wet season.

The dry season in the wet-dry tropics of northern Australia is a critical period for toad survival. During this time the relative humidity decreases, rainfall is infrequent and the rate of water loss probably increases. Dehydration at this time may be the major cause of toad mortality (Zug and Zug 1979). Also, if this season is extended or particularly severe, shelter sites may not be enough to protect toads.

The availability and number of shelter sites can therefore limit the number of toads active in a population especially during the dry season (Straughan 1966). Shelter sites may consist of shallow dugouts, logs, piles of debris, dry or moist grass, or burrows and allow toads to avoid high temperatures and extremely dry conditions. For *B. marinus* in tropical regions, lack of adequate shelter can result in death by dehydration when combined with an extended dry season (Zug and Zug 1979). Schwarzkopf and Alford (1996) demonstrated that *B. marinus* in the wet-dry tropics choose shelter sites that provide protection from desiccation and the type of sites chosen changed with season. For instance, toads use burrows frequently during the dry season whereas little or no preference for any shelter type was observed during the wet season. They showed that toads do not remain in one shelter for long periods (mean length of stay three days) in any season and that this behavioural adaptation and depressed activity decreases the risk of desiccation. However, toads often returned to quality shelter sites, eg. burrows, and were an important resource during the dry season. In addition to protection from desiccation, burrows may also provide toads with protection from predators and/or high temperatures (Schwarzkopf and Alford 1996).

The dry season is presumed to limit toad populations due to long dry periods and characteristic high temperatures. Toads in northern Australia must survive through the dry season and breed in the following wet season when conditions (eg. food and water availability) become suitable. In addition to reduced activity, toads must locate a suitable retreat site. Chapters 3 to 6 in this thesis examine the variations in toad activity, growth, survival, and body condition in relation to the contrasting climatic conditions of the wet-dry tropics. Many of these ecological characteristics suggest that retreat or shelter sites in the wet-dry tropics are possibly a limiting resource for toads. The characteristics of toad retreat sites however, are relatively unknown and are therefore examined in an enclosure experiment in Chapter 7. This experiment was designed to provide insights into the type and characteristics of toad shelter sites, whether they show site fidelity once a favourable site has been located, and if toads will then aggregate in shelters.

1.9 Aims of this Study.

Specifically, this study is directed at examining and comparing the population ecology of the terrestrial stage of *B. marinus* between a population at Calvert Hills in the Gulf of Carpentaria of the Northern Territory (17° 45′ S; 137° 19′ E; first colonised by toads in 1985) and a population in the Townsville region (19° 21′ S; 145° 36′ E; first colonised by toads in 1937).

This study examined

a. the biotic and abiotic factors that affect growth, survival and activity of *B. marinus* metamorphs (Chapter 3);

b. the growth rates and effects of abiotic and biotic factors on growth of sub-adult and adult *B. marinus* at Calvert Hills and in the Townsville region (Chapter 4);

c. the size and structure of *B. marinus* populations active alongside water sources, and factors that affect populations at Calvert Hills and in the Townsville region (Chapter 5);

d. the number of *B. marinus* from different age categories active at a water source, and seasonal changes in their activity in populations at Calvert Hills and in the Townsville region (Chapter 5);

e. the seasonal trends and changes of individual body size of *B. marinus* at Calvert Hills and in the Townsville region (Chapter 5);

f. the seasonal trends and changes in the body condition of *B. marinus* at Calvert Hills and in the Townsville region (Chapter 6); and

g. the variation in retreat site selection and the spacial distribution and site fidelity shown by *B. marinus* to retreat sites (Chapter 7).

The cane toad, *B. marinus*, is a recognised pest species in Australia. This study was undertaken to determine ecological characteristics of populations of the terrestrial stage of the toad in the wet-dry tropics of northern Australia. Ecological factors of toad

populations such as growth, survival, activity patterns, seasonal changes in body size and condition and characteristics of limiting resources (eg. shelter sites), were examined by a long-term mark-recapture program and specific field experiments.

In addition to filling some of the known gaps of current knowledge, the investigation into the ecology of the terrestrial stage of the cane toad's life cycle may provide baseline data and highlight areas where biological control factors may be most beneficial. For example, if a microorganism control agent is developed (ie. bacteria or virus), this would be best targeted at times when toads are most vulnerable to diseases. Zug and Zug (1979) suggested that when toads first emerge from water as small metamorphs they are considerably more vulnerable to disease and predators. Their study further hypothesised that toad populations in the seasonal tropics are under severe hydric stresses late in the dry season. This results of this study on the ecology of toad populations aims to identify susceptible periods in the terrestrial life cycle of *B. marinus* populations.

Other methods of biological control may be designed for toad populations. For example, sterilising one sex of a pest species has been a successful method for controlling some animal populations. Although this method is unlikely, if male or female toads were targeted for sterilisation then it would be important to have ecological information on their activity including the period when the maximum number of each sex within a population could be easily targeted. This study aims to demonstrate seasonal variation in male and female toad activity and identify times when the highest numbers of each sex are active around water sources in the wet-dry tropics.

The ultimate aim of describing these ecological characteristics of cane toad populations is therefore to provide quantitative information for examination of possibilities for biological control of the species. Depending on the particular type of control method

used, the demographic information on the terrestrial stage of the toad provided in this study will therefore provide an insight into the practicality of controlling the toad.

In summary, the aims of this study are to document and compare the number of toads active at a water source, the dynamics of toad populations, and factors controlling numbers of the terrestrial stage of *B. marinus* in two separate, but climatically different, locations of the wet-dry tropics of northern Australia and provide baseline ecological data for some type of control of their populations.

Chapter 2. Study Sites.

This study was conducted on Calvert Hills Station in the Gulf of Carpentaria, Northern Territory (Locality 1), and several sites south and west of Townsville, north Queensland (Locality 2) (Figure 2.1). Both locations differed in the time since *B. marinus* had colonised with toads first recorded around the Townsville region in 1937 (Freeland 1986a) and at Calvert Hills in 1985. An additional locality, Fletcherview Station (19° 52.5′ S; 146° 10.5′ E), north-west of Charter's Towers approximately 95km SW of Townsville, north Queensland, was used for the enclosure experiment described in Chapter 3.

2.1 Calvert Hills Station.

Calvert Hills Homestead is located 17° 25′ S; 137° 03′ E; 90km west of the Queensland and Northern Territory border (Figure 2.1) in the Gulf of Carpentaria of northern Australia. This region is characterised by distinct wet and dry seasons and high daily maximum temperatures. The station is 4833km^2, and situated approximately 100km south of the coast of the Gulf of Carpentaria. The property is a cattle station and consists of regions of rocky escarpments divided by rivers and creeks and black-soil plains. The vegetation is primarily associated with sandstone habitats (eucalypt woodland-scrubland), and black-soil eucalypt communities (open forest and open woodland) (Brock 1988). The two main sites at this location were located alongside rivers and were subjected to occasional grazing by cattle.

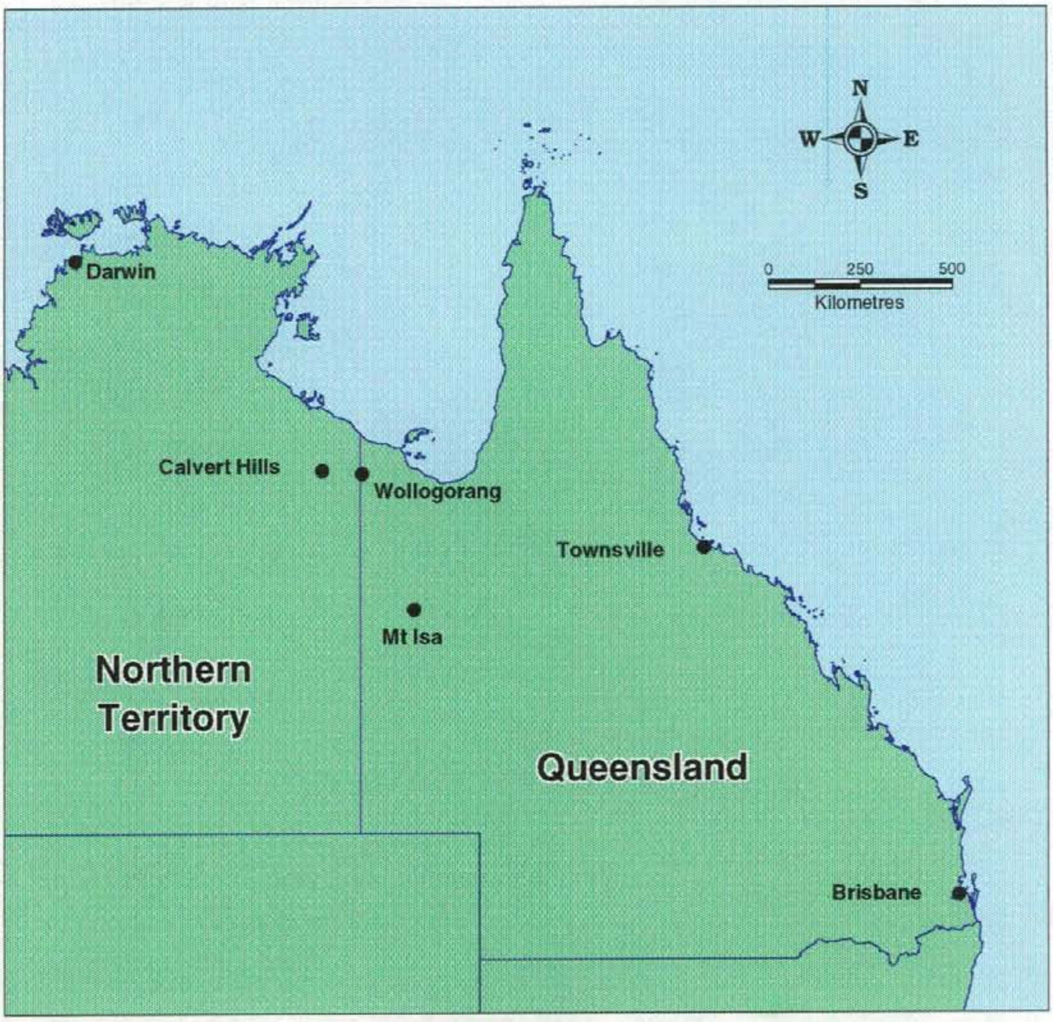


Figure 2.1. Map of Queensland and the Northern Territory showing the location of Calvert Hills and Wollogorang Stations (NT), Townsville sites (QLD) and Fletcherview Station.

2.1.1 Calvert Hills Sites.

Two major sites, Big Calvert River (17° 13′ S; 137° 26′ E), and Homestead (17° 45′ S; 137° 19′ E) were situated on the Big Calvert and Little Calvert River respectively (Figure 2.2), and were used for the mark-recapture study at Calvert Hills. These two sites, are separated by 15 approximately kilometres of rocky, open eucalypt forest and grassland. Both the Little and Big Calvert Rivers are intermittent water courses, and usually consist of isolated pools bounded by large paperbarks (*Melaleuca* sp.), figs (*Ficus* sp.), and ghost gums (*Eucalyptus papuana*). These rivers only flow after heavy rain during the wet season.

An additional site, located on the Little Calvert River (17° 12.5′ S; 137° 22′ E), was used for the enclosure experiment detailed in Chapter 3.

2.1.2 Calvert Hills Sampling Dates.

Sampling at Calvert Hills commenced in November 1986 and continued through to April 1992; however no sampling occurred in 1990. Twelve sampling trips at two major sites, Big Calvert River and Homestead, were undertaken during this time. A sampling trip usually consisted of three samples per site, while one sample is equivalent to a single nightly census. A summary of sampling trips is provided in Appendix 1.

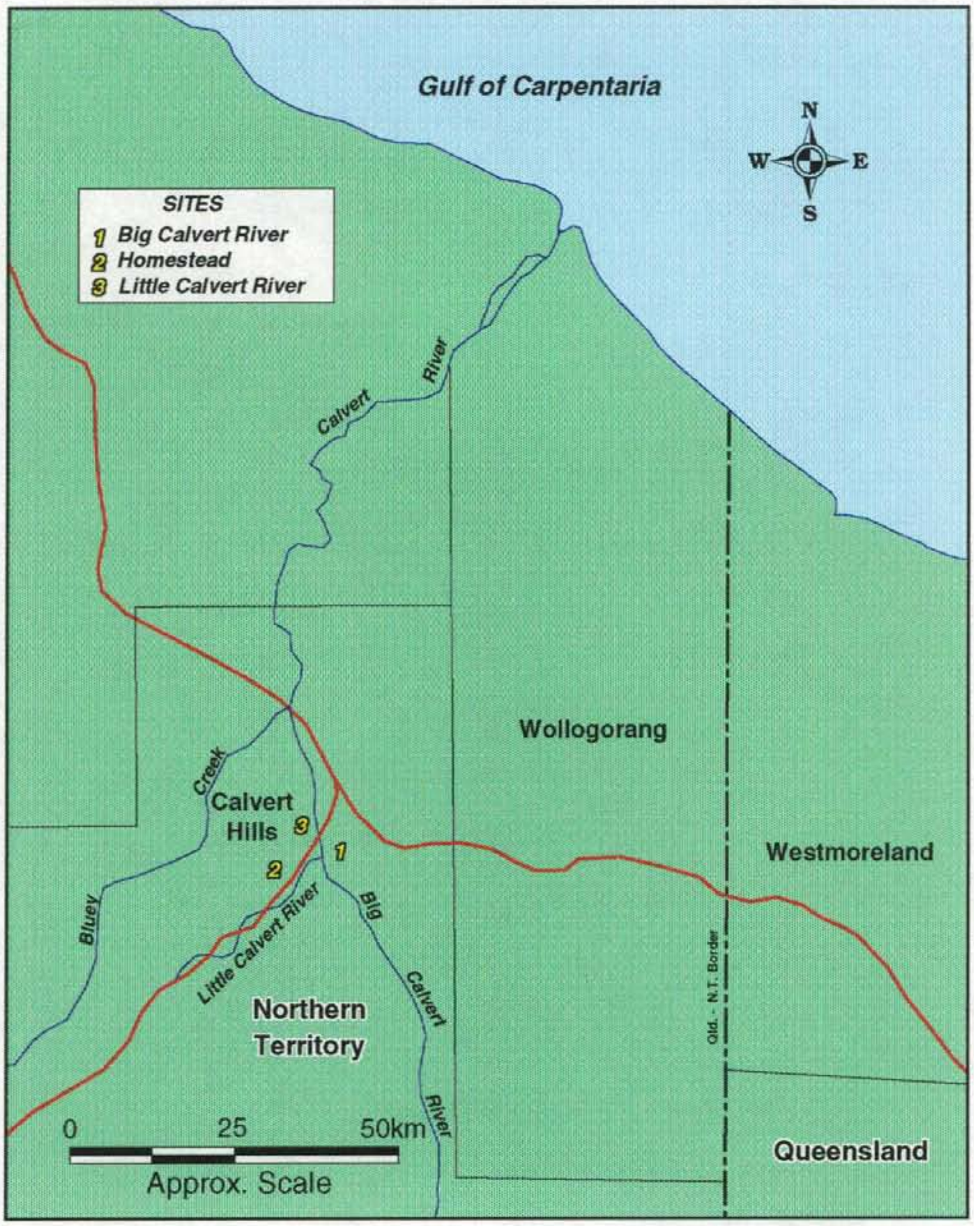


Figure 2.2. Map showing location of sites used at Calvert Hills.

2.2 Townsville Region.

The Townsville region is approximately 1450 kilometres north of the Queensland capital, Brisbane, and is characterised by warm and sub-humid conditions with a distinct summer rainfall maximum. Although coastal, the Townsville region is subject to wet and dry seasons and is surrounded by predominately dry, open sclerophyll and eucalypt forest and grassland. All three Townsville sites consisted of earthen dams with the surrounding area subjected to cattle grazing.

2.2.1 Townsville Sites.

Three main sites, Bentley Lagoon (19° 22′ S; 146° 55′ E), Rock Road Dam (19° 18′ S; 146° 36′ E), and Bell's Dam (19° 18′ S; 146° 40′ E), were used for the mark-recapture study (Figure 2.3). Each site consisted of an earthen dam that had little or no vegetation around their immediate edge with the surrounding area consisting of dry, open eucalypt forest dominated by *Eucalyptus platyphylla* and *E. drepanophylla*. Two sites were situated west of Townsville (Rock Road and Bell's Dam), and one site was south of the town (Bentley Lagoon) (see Figure 2.3). Water levels in each dam fluctuated from season to season, with Bell's Dam and Bentley Lagoon levels assisted by a pump. The location of each transect around each dam was adjusted according to the water level so the area sampled was equivalent to a 10 x 100 metre transect (see Figure 4.1). Bell's Dam dried up after March 1992 and was not refilled and the site was therefore not used for the study after this time.

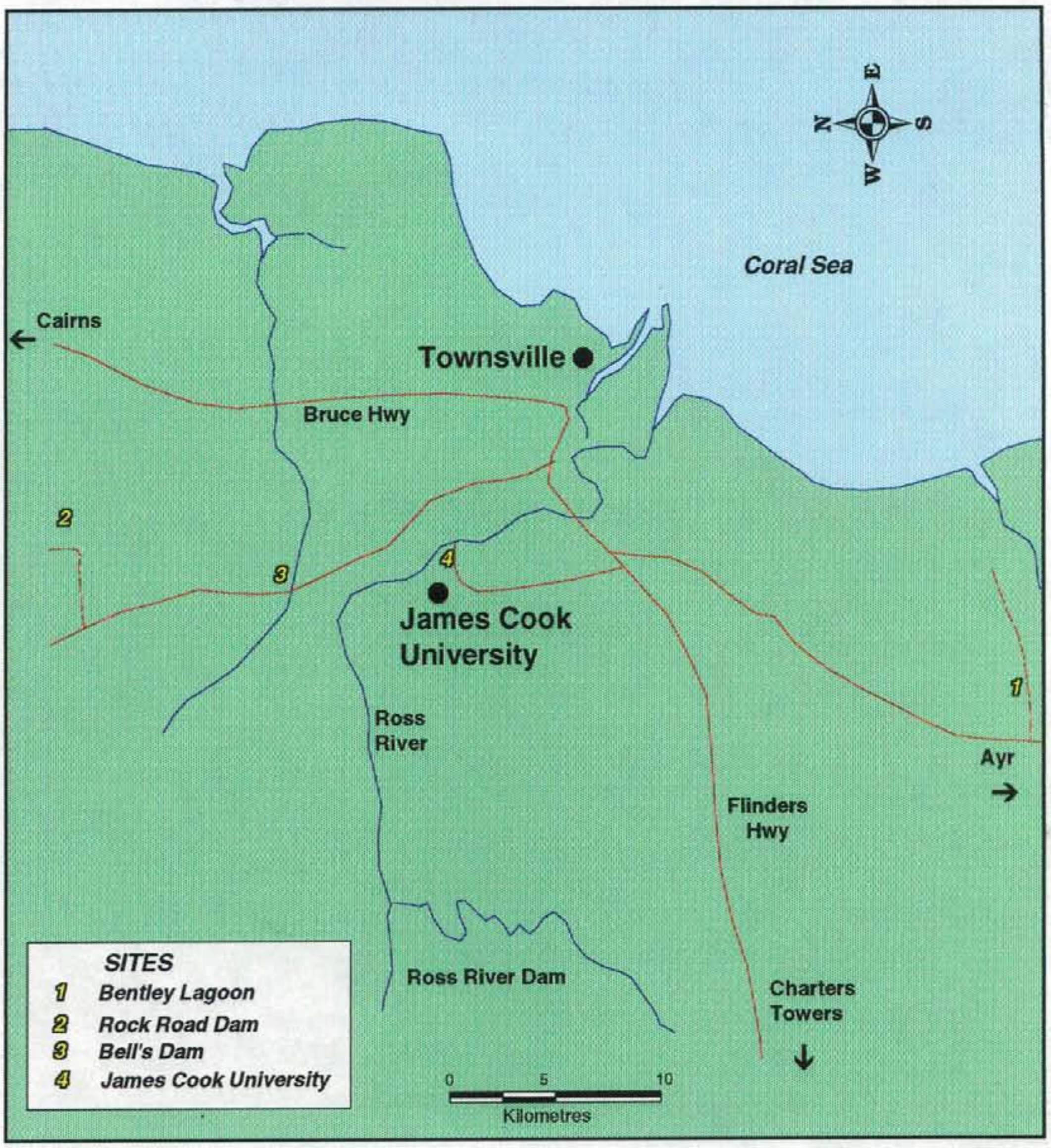


Figure 2.3. Map showing location of Townsville sites.

2.2.2 Townsville Sampling Dates.

Townsville sampling commenced in November 1986 and continued through to January 1993; however, no samples were taken during 1990. Twenty-two sampling trips were undertaken at Townsville sites during this period. A sampling trip usually consisted of three samples per site, while one sample is equivalent to a single nightly census. The their details of these sampling trips are shown in Appendix 2.

2.3 Climate.

2.3.1 Rainfall.

Calvert Hills and Townsville have tropical wet-dry climates consisting of distinct wet and dry seasons (Figure 2.4). Rainfall is distinctly seasonal with wet seasons often of short duration and unreliable development followed by a long, generally dry remainder of the year (Oliver 1978). The annual average rainfall at Calvert Hills was 581mm (data from records kept at Calvert Hills Homestead between 1980 to 1989), considerably lower than the annual average (1039mm) recorded at Townsville over 25 years (data from Townsville Bureau of Meteorology between 1967 to 1992). Ninety percent of the Calvert Hills annual average rainfall, and 80% of Townsville annual average rainfall, occurs between the months of November and March, and these months were classified as the wet season. The remaining months, April to October, account for less than 10% of Calvert Hills average annual rainfall and less than 20% of Townsville's average annual rainfall, were classified as the dry season. The rainfall recorded at Calvert Hills, Wollogorang Station and Townsville during the study (1986-1993) are presented in Appendix 3.

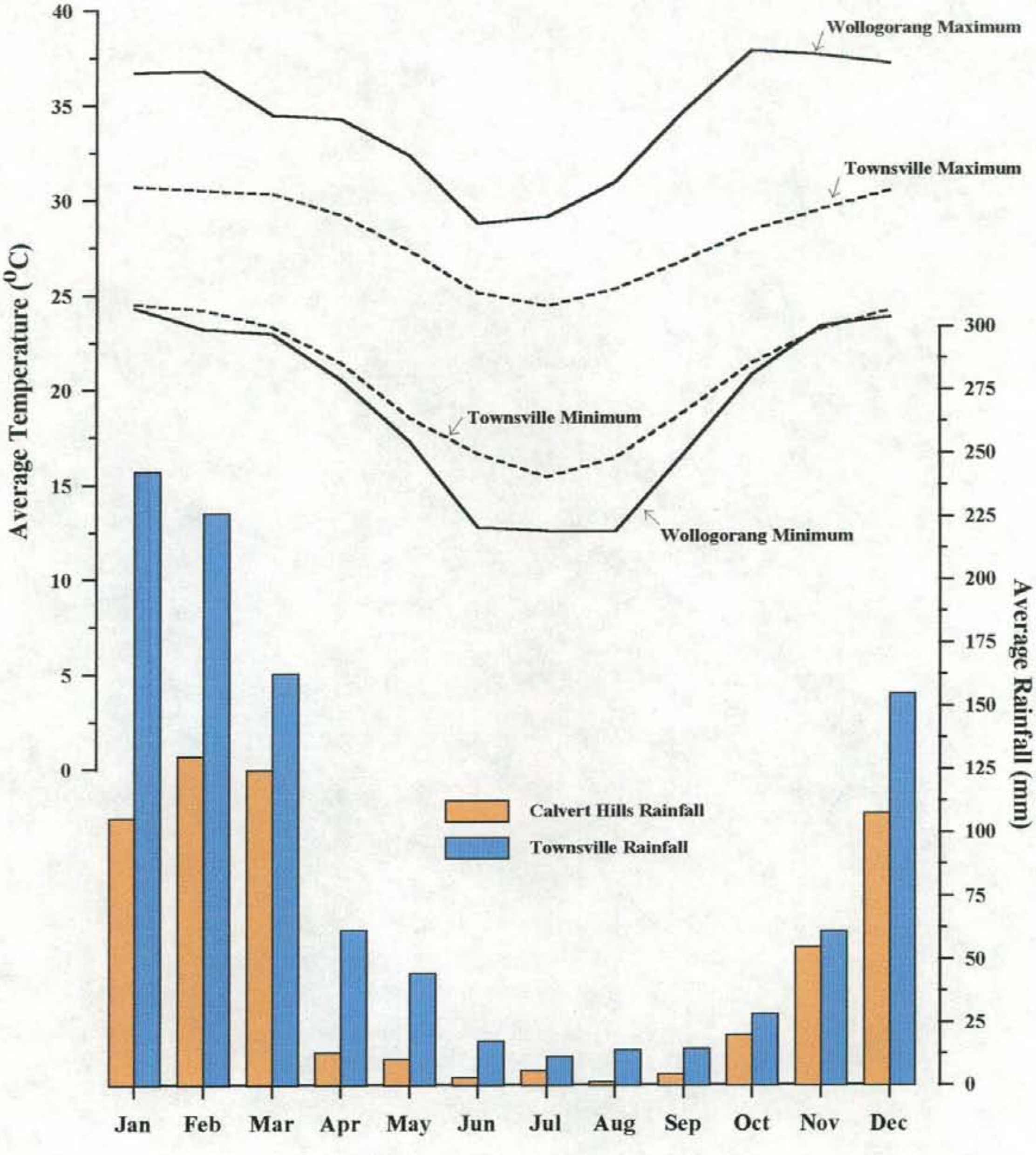


Figure 2.4. Average rainfall for Calvert Hills (red bars) and Townsville (blue bars), and mean maximum and minimum temperatures for Wollogorang Station (solid lines) and Townsville (dashed lines).

Each sample was categorised into one of five separate seasons based on the amount of rain 90 days previous to the sampling date, and the amount of rain in the following 30 days since the sampling date (Table 2.1). Each sample was designated within the early-wet, middle-wet, late-wet/early-dry, middle-dry or late-dry season.

The early-wet season represents the first major rainfall events, often storms, after the dry season and was characterised by rainfall between 50 and 150mm in the previous 30 days and between 25 and 200mm of rain in the following 30 days. The middle-wet season occurs during the height of the wet season and characteristically has high rainfall (up to 500mm) during the previous 30 days and high rainfall (up to 400mm) during the following 30 days. The late-wet/early-dry season corresponds to the end of the wet season and the commencement of the dry season and was characterised by high rainfall (up to 300mm) during the previous 30 days and low rainfall (from 0 to 50mm) during the following 30 days. The middle-dry season occurs in a period with very little rainfall (from 0 to 50mm) during the following 30 days and moderate rainfall (50-100mm) during the previous 30 days corresponding to the end of the wet season. The late-dry season has very little rainfall (from 0 to 50mm) during the previous 90 days or the following 30 days.

Table 2.1. Criteria for division of seasons and number of trips during each season at Calvert Hills and Townsville.

Season Number	Season Title	Previous 90 Day Rainfall (mm)	Following 30 Day Rainfall (mm)	Number of Trips	
				Calvert Hills	Townsville
1	Early-wet	50-150	25-200	2	4
2	Middle-wet	150-500	50-400	2	5
3	Late-wet/Early-dry	100-300	0-50	5	4
4	Middle-dry	50-100	0-50	1	3
5	Late-dry	0-50	0-50	2	8

2.3.2 Temperature.

Maximum and minimum temperature records were not kept at Calvert Hills. Consequently records kept at Wollogorang Station, approximately 50km east of Calvert Hills Station (see Figure 2.1), from 1986 to 1990, were used. Townsville temperature records from 1980 to 1992 were from readings taken by the Bureau of Meteorology at the Townsville Airport. Both rainfall and temperature records for the Calvert Hills and Townsville regions are illustrated in Figure 2.4.

The average monthly maximum temperatures in the Calvert Hills region are well above that at Townsville with mean temperatures over 35° C during October to December, while the average minimum temperatures are similar to Townsville except from June to September where they are considerably lower (Figure 2.4). The average monthly rainfall patterns at both locations are similar except for more rain per month, including more rain during the dry season, at Townsville compared to Calvert Hills.

Chapter 3. Metamorph Growth, Survival and Activity Patterns.

Abstract

Factors affecting the growth and survival of post-metamorphic *Bufo marinus* were examined using quadrat sampling and enclosure experiments. *Bufo* metamorphs, defined as newly emerged terrestrial toads between 8 and 29mm snout-vent length (SVL), were classified into four stages on the basis of colour and size. The mean densities of all metamorphs during both seasons at 2-3 m and 4-5 m from water were $0.8/m^2$ and $0.6/m^2$ respectively. Stage 2 metamorphs were most common in samples. Most stage 1 metamorphs occurred within 1 m of the water in both seasons (98% wet; 95% dry). Increasing percentages of stage 2, 3 and 4 metamorphs occurred in samples 2-3 and 4-5 m from water (38, 49, and 80%, respectively, averaged over both seasons).

Three experiments, with initial metamorph densities of 3.3, 6.7 and $16.7/m^2$, examined the response of metamorph growth and survival rates to density and showed that metamorphs in the lower density enclosures grew more rapidly than metamorphs in the higher density enclosures. A profile analysis showed that daily survival rate was not density-dependent. Correlation analyses showed that daily metamorph survival was influenced by daily maximum and minimum temperatures. Metamorphs at lower densities attain juvenile size (30mm) more rapidly and, because they survive at the same daily rates as metamorphs at higher densities, they experience lower cumulative mortality than high density metamorphs.

3.1 Introduction.

The timing of amphibian metamorphosis may be controlled by selective tradeoffs between growth rate and mortality risks in the aquatic and terrestrial habitats (Werner 1986; Ludwig and Rowe 1990; Rowe and Ludwig 1991). Information on growth and survival immediately after metamorphosis is sparse. Most studies of anurans consider the terrestrial adults or the aquatic larvae. Although many studies have examined the processes of larval growth and metamorphosis (Wilbur and Collins 1973; Alford in press), few have studied activity, survival or growth from metamorphosis to adult size (Smith 1987; Breden 1988).

The cane toad, *Bufo marinus*, has a short aquatic larval stage (approximately 14-60 days; Tyler 1989), and metamorphoses at a relatively small body size, (approximately 8-11mm; Werner 1986; Zug and Zug 1979). At metamorphosis many features such as the heart, lungs and aerobic capacity are poorly developed in *Bufo* (Pough and Kamel 1984). Post-metamorphic growth in *B. marinus* accounts for about 99.9% of the adult mass (Werner 1986). Emergence onto land at a very small size may be an adaptation to minimise larval mortality risks such as pond drying, or may allow faster growth in the terrestrial habitat.

Although growth rates may be high on land, high mortality may occur in the very young because of their small size (Clarke 1974). At small sizes, recently metamorphosed amphibians often must remain near the edge of water bodies (Clarke 1974; Licht 1974). The growth and survival of amphibian metamorphs may be affected by biotic factors such as competition, predation or pathogens (Licht 1974; Berven 1990; Freeland and Kerin 1991), or abiotic factors (Berven 1990), including pond drying (Semlitsch and Wilbur 1988; Freeland and Kerin 1991), and the interactions between drying and biotic factors (Pechmann *et al.* 1989).

The toxicity of *B. marinus* may be lowest between metamorphosis and the full development of skin glands; resulting in high mortality rates through predation (Zug and Zug 1979; Claussen and Layne 1983). Zug and Zug (1979) suggested that post-metamorphic mortality in *B. marinus* was high and was probably caused by predation, drowning, developmental abnormalities, dehydration, and starvation.

The growth and survival rates of post-metamorphic anurans can also be affected by seasonal variation in temperature and precipitation. Clarke (1974) suggested that these factors may not strongly affect immature *Bufo fowleri*, but Zug and Zug (1979) suggested that recently metamorphosed *B. marinus* in tropical regions grow rapidly during the first half of the wet season, and that growth slows or ceases during the dry season (Zug and Zug 1979).

A recent study by Berven (1990) demonstrated that body size, age, population density, precipitation levels and predator abundance all had significant effects on the survival of juvenile *Rana sylvatica*. Rainfall, temperature, and day length may also affect the early stages of post-metamorphic development, as ambient temperatures influence rates of growth and water loss (Richards and Lehman 1980). Freeland and Kerin (1991) concluded that the activity of *B. marinus* metamorphs near water is greatest on moist substrates at high daytime temperatures in windy weather. They also revealed that activity is diurnal but becomes nocturnal in the juvenile stages.

How biotic and abiotic factors affect the growth and survival of *B. marinus* metamorphs was not known. This study therefore investigated:

a. the density, activity patterns, and movements of *B. marinus* metamorphs at the edge of their natal ponds during dry and wet seasons;

b. the growth and survival rates over the first 18 days of terrestrial life of *B. marinus* metamorphs at various densities; and

c. correlations between variation in the abiotic environment and the growth and survival of metamorph populations.

3.2 Methods.

3.2.1 Study Area.

Quadrat sampling and enclosure experiments were conducted between January and June 1988 at Calvert Hills. Sites were located on the Little Calvert and Big Calvert Rivers (section 2.1.1). Data were collected over three week periods during the wet season (January/February) at the Little Calvert River, and during the early dry season (May/June) at the Big Calvert River (the Little Calvert River was dry in May/June and the Big Calvert River was selected as it was similar habitat). Sites were characterised by sandstone banks vegetated by *Melaleuca* and *Pandanus*, surrounded by dry open *Eucalyptus* woodland. The river banks slope gently (15°) towards the water and mainly consisted of mud and bare soil.

An additional enclosure experiment was performed on Fletcherview station (see Figure 2.1), approximately 95km south-west of Townsville. This site was a side pool of the Burdekin River, and consisted of a gently sloping, sandy bank, with a relatively thick grass cover between one and five metres from the water's edge. The area at the water's edge was bare and consisted of moist mud and sand.

3.2.2 Quadrat Sampling.

To determine the approximate natural density of metamorphs (see Section 3.2.3), quadrat samples of metamorphs were taken between the edge of the water to a distance of three metres. All sampling was conducted between one and three hours after sunrise and at two-day intervals over two 18-day sampling periods. A 1 x 1 m metal quadrat, 20cm high, was used to measure the densities of *B. marinus* metamorphs (SVL <30mm) along 100 m transects. Twenty individual quadrat samples were taken at each distance, (0-1, 2-3 and 4-5 m) from the water on each sampling day. The locations of the samples along the 100m transect were determined using random numbers on each sampling date.

Metamorphs were classified into four stages based on size and external features. These stages were: stage 1, black dorsum, SVL about 8-12mm; stage 2, dorsum mottled with small orange spots, SVL about 12-16mm; stage 3, fine white mid-dorsal line, SVL about 16-25mm; stage 4, enlarged parotoid glands, SVL about 25-29mm. Similar changes with size, colour and pattern were noted by Freeland and Kerin (1991). Climatic data (air, soil, water, and maximum/minimum temperatures, humidity and rainfall) were recorded on each sample occasion.

The data were analysed using a hierarchical maximum-likelihood multiway frequency analysis (Bishop *et al.* 1975). This uses log-linear models to produce a series of tests analogous to tests of main effects and interactions in an analysis of variance. The analysis examined how the observed number of metamorphs was divided among stages, seasons, and distances from water, and how these categories interacted in influencing the observed number of metamorphs.

To determine if the distribution of metamorphs near water is due to biased random movement (ie. diffusion), away from water over time, combined with the growth and

development of metamorphs, a pascal program (developed by R. Alford), was used to examine the stage-specific differences in distributions of metamorphs near water.

3.2.3 Enclosure Experiments.

Enclosure experiments were performed during the wet (January 1988) and dry seasons (May 1988) at Calvert Hills, and during the dry season (June 1989) at Fletcherview. Fifteen 1 x 3 m rectangular enclosures were placed with one shorter edge next to the water. Each enclosure consisted of 1 m high fly-screen stapled around six wooden stakes. The wooden stakes were hammered into the ground so the bottom of the fly-screen was buried approximately 3-5 cm into the soil. All *B. marinus* metamorphs were then cleared from inside the enclosures.

Five replicates of three metamorph densities were used. Each block of three cages, contained one cage at each density. The densities of metamorphs used were 3.3, 6.7, and 16.7/m^2. The lowest density is similar to the mean density of metamorphs found during the quadrat sampling. Stage 2 metamorphs for each experiment were collected from the area. Individuals were then selected haphazardly, measured, and assigned to enclosures.

The enclosures were sampled every 48 hours for up to three weeks. Each time, enclosures were thoroughly searched and all surviving metamorphs were collected, counted and individually measured to the nearest millimetre. Potential predators in each enclosure were noted but not disturbed. Once data were recorded, metamorphs were replaced into their original enclosure.

The data were analysed using profile analyses of patterns of growth and survival. Profile analysis allows analysis of repeated measures data, such as the growth and survival

over time, while conducting a set of tests that are equivalent to those done in an analysis of covariance (ANCOVA) where time is the covariate (Simms and Burdick 1988). It combines two tests: an analysis of variance (ANOVA) of responses totalled over time that is analogous to tests for differences between intercepts in an ANCOVA, and a multivariate analysis of variance (MANOVA) of differences between times that is analogous to tests for differences between slopes in an ANCOVA. The profile analyses examined the effects of experiment (which include season, wet versus dry, and region, Calvert Hills versus Fletcherview), density, and the interaction of experiment with density on metamorph survival and growth rates. In these analyses, the analysis of totals examined how total survival or growth through the experiment responded to the treatments, while the analysis of differences examined the response of the temporal pattern of survival or growth. To interpret the mechanisms that might be causing these responses, correlations of two responses (percent size increase/48-hours and percent survival/48-hours) were examined, with four environmental variables (number surviving in the enclosure, maximum temperature, minimum temperature, and rainfall). Correlations using the entire data set were performed to determine the overall importance of the environmental variables including a correlation using the difference between maximum and minimum temperature (ie. an index of relative cloud cover). There was no rain during the Calvert Hills dry season experiment, so rainfall could not be meaningfully included in the overall analysis.

To examine seasonal and site variation and the effects of rainfall, a separate analysis was also performed for each experiment. Mean growth and survival rates were used in models of *B. marinus* population dynamics and linear regressions were used to relate proportional growth/day to biomass/m^2. These regression equations and mean values for daily survival were used to simulate growth and survival from 10 mm to 30 mm SVL in each treatment of each experiment. These simulations allowed a prediction of the time taken for standard-sized metamorphs would have required to reach 30mm SVL, and what proportion would have survived to that size.

3.3 Results.

3.3.1 Quadrat Sampling.

During the wet season and early dry season 648 and 699 metamorphs respectively, were counted and staged. Of these, 90% (wet season) and 77% (dry season) were at stage 2. The mean numbers of each metamorph stage at the three distances from water are summarized for the wet and early dry season in Table 3.1.

Table 3.1. The density (individuals per 100 m²) of metamorphs of different stages at three distance from the water's edge during the wet and dry season. (Sample size = 20 for each distance from water).

Distance from Water (m)	Stage 1		Stage 2		Stage 3		Stage 4		Total	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Wet Season										
0-1	28.8	5.2	223	17.4	4.4	2.2	0	0	256	19.1
2-3	0	0	79.4	10.5	1.3	0.9	0	0	80.6	10.5
4-5	0.6	0.6	58.7	7.7	0.6	0.6	5	1.7	65	8
Dry Season										
0-1	33.1	6.1	188	12.9	14.4	3.1	1.3	0.9	236	16
2-3	0	0	65	8.7	15	3.8	0	0	80	9.6
4-5	0.6	0.6	41.2	7.7	13.1	3	1.3	0.9	56.2	9.5

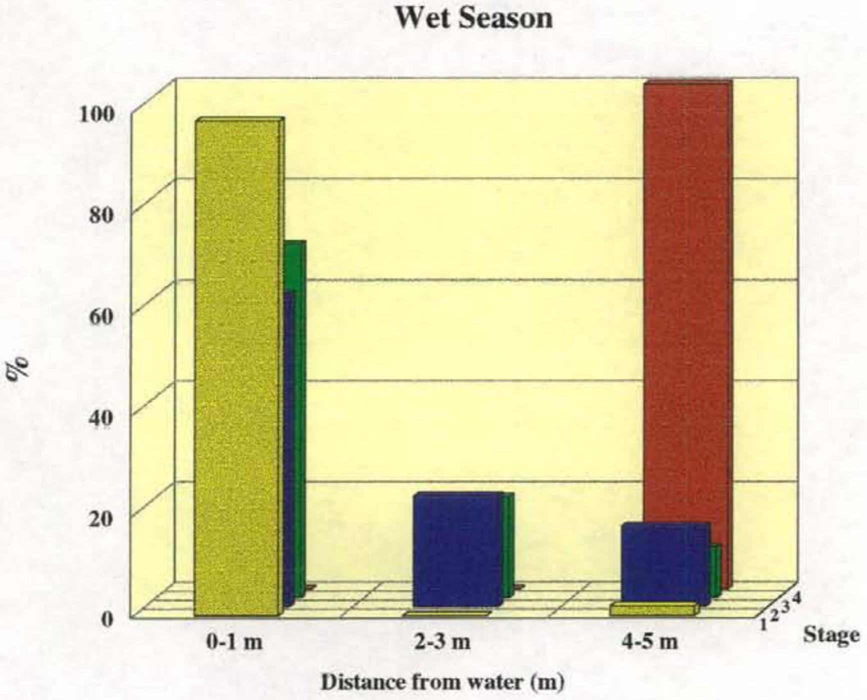
The total number of metamorphs captured in quadrat samples was influenced most strongly by stage (Table 3.2). The majority of metamorphs captured were at stage 2 (Table 3.1), with stage 1 accounting for the next highest number. Distance also affected the numbers captured with more captured within 1 m of the water than at either of the other distances. Approximately equal total numbers were captured in both seasons (Table 3.1).

Two of the interactions (season by stage and distance by stage, Table 3.2) were also significant. These indicate that the distribution of metamorphs among stages varied both seasonally and with distance from water. In both seasons, nearly all of the smallest metamorph class (stage 1) were found at the water's edge. At the other distances sampled (2-3m and 4-5m), the mean number of stage 1 metamorphs was $\leq 0.01/m^2$. Most stage 2 metamorphs also occurred within 1 m of water, but their numbers declined more gradually as the distance to water increased. Larger metamorphs (stages 3 and 4) were somewhat more evenly distributed over the three distances from water, and were more abundant in the dry season samples.

The percentage of the number of metamorphs at each stage found at each distance from water in each season are illustrated in Figure 3.1. Stage 1 metamorphs were primarily encountered 0-1 m from water, accounting for 98% (wet season) and 95% (dry season) of those observed. During the wet season, stage 4 metamorphs were found only at the 4-5m distance from water. They were more evenly distributed away from water in the dry season. Seventy percent of stage 3 metamorphs were found at 0-1m from water during the wet season, but were evenly distributed at the three distances during the dry season. The spatial distribution of stage 2 metamorphs was similar in both seasons. Stage 2 metamorphs were primarily found at the 0-1m distance (62% for both seasons) and decreased at the next two distances from water.

Figure 3.1. The percentage of the number of metamorphs at each stage (1-4) found at each distance from water in the wet- and dry-season samples at Calvert Hills during 1988. Each colour represents one of the four size-specific stages of metamorph:

Yellow = stage 1 metamorph;
Blue = Stage 2 metamorph;
Green = Stage 3 metamorph;
Red = Stage 4 metamorph.


Wet Season
100
80
60
40
20
0
%
0-1 m
2-3 m
4-5 m
Distance from water (m)
1
2
3
4
Stage

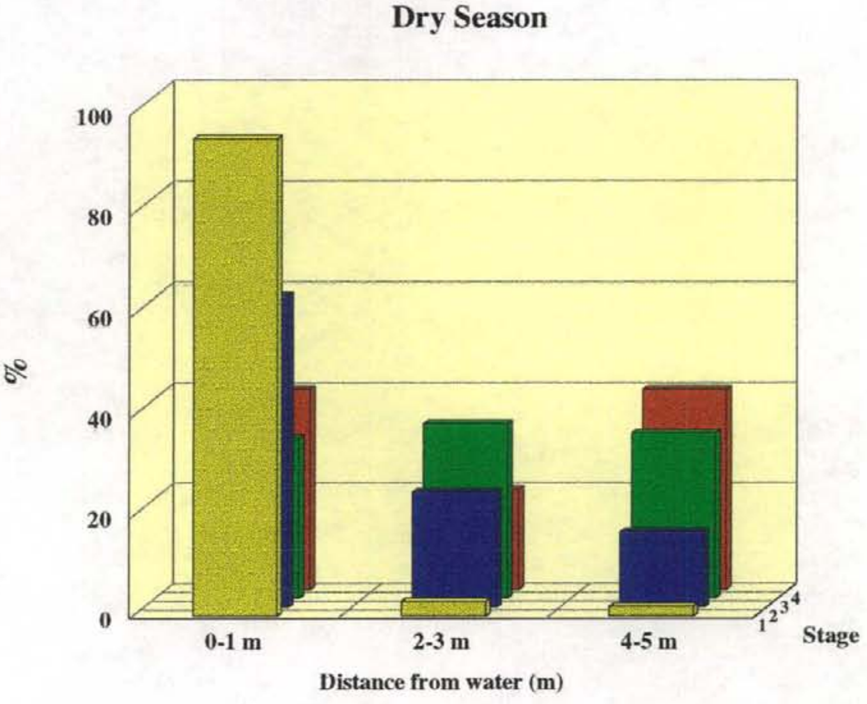

Dry Season
100
80
60
40
20
0
%
0-1 m
2-3 m
4-5 m
Distance from water (m)
1
2
3
4
Stage

Table 3.2. Hierarchical maximum-likelihood multiway frequency analysis (Bishop *et al.* 1975) of numbers of metamorphs in wet- and dry-season quadrat samples, classified by season, distance from water and stage of growth. (* = significant at 0.05 level).

Source	d.f.	χ^2	*P*
Season	1	1.78	0.1829
Distance	2	450.77	<0.0001*
Stage	3	1123.17	<0.0001*
Season*Distance	2	0.8	0.6703
Season*Stage	3	59.87	<0.0001*
Distance*Stage	6	127.18	<0.0001*
Season*Distance*Stage	6	10.41	0.1084

The random movement analysis commenced with 10,000 age zero metamorphs at the edge of a water body with the movement of each metamorph on each day simulated by first choosing a random number from a uniform distribution on the interval (0,1), representing movement of 0 to 1 metre. The program then subtracted a constant from this random number so that movement could be towards (negative) or away from (positive) water. Movements that resulted in locations less than 0 metres from water were truncated random walk with no bias. For example, using a constant of 0.45 resulted in a random walk biased toward movement away from the edge of a water body at an average of 0.05 metres (ie. 5cm) per day. The distances of all 10,000 simulated metamorphs were classified into 1-metre intervals matching those used for real animals on days when the growth models predicted that animals would reach the median size for each of four classes (wet season: days 5, 16, 33 and 46; dry season: days 8, 30, 64 and 93).

3.3.2 Enclosure Experiments.

3.3.2.1 Patterns of Survival.

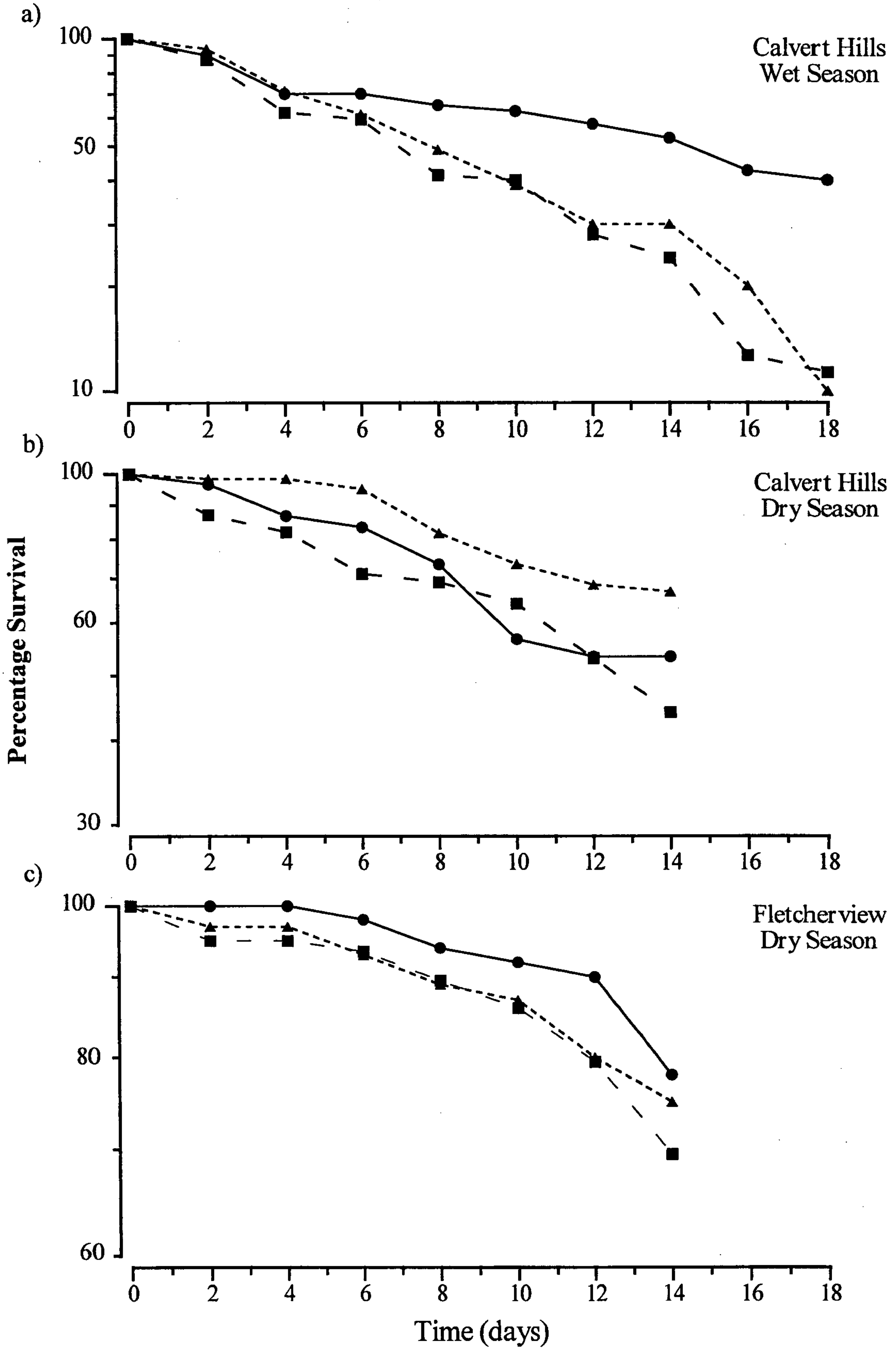
Experiment (season confounded with region) significantly affected total metamorph survival (Table 3.3; Figure 3.2). Density and the experiment by density interaction did not affect total metamorph survival. However, the time by experiment interaction affected metamorph survival (Table 3.3; Figure 3.2). This shows that the number surviving decreased through time, and that the pattern of this decrease differed among the three experiments.

Table 3.3. Profile analysis of survival rates of metamorphs in the enclosure experiments. (* = significant at 0.05 level).

	Mean Square	Wilkes' λ	d.f.	F	*P*
Analysis of Totals (ANOVA)					
Experiment	12096.47		2	28.39	0.0001*
Density	995.17		2	2.34	0.1183
Experiment*Density	434.16		4	1.02	0.4175
Error	426.07		24	-	-
Analysis of Differences (MANOVA)					
Time		0.03	718	74.22	0.0001*
Time*Experiment		0.19	1436	3.37	0.0016*
Time*Density		0.54	1436	0.92	0.5458
Time*Experiment* Density		0.35	2866	0.81	0.7255

Figure 3.2. The percentage of metamorphs surviving in enclosure experiments at initial densities of 3.3 m^{-2} (●, solid line), 6.7 m^{-2} (▲, short dashed line), and 16.7 m^{-2} (■, long dashed line). (Note that the ordinate of each graph is on a log scale).

a) Calvert Hills, in January-February 1988;
b) Calvert Hills, April-May 1988;
c) Fletcherview, June 1989.


a)
100
50
10
Calvert Hills
Wet Season
0
2
4
6
8
10
12
14
16
18
b)
100
60
30
Calvert Hills
Dry Season
Percentage Survival
0
2
4
6
8
10
12
14
16
18
c)
100
80
60
Fletcherview
Dry Season
0
2
4
6
8
10
12
14
16
18
Time (days)

The time by density and time by density by experiment interactions did not significantly influence metamorph survival.

At all densities, survival to the end of the experiment was highest in experiment 3, intermediate in experiment 2, and lowest in experiment 1 (wet season; Figure 3.2). The interaction of experiment with time in the MANOVA analysis (Table 3.3) is apparent. For example, in the Calvert Hills wet season (Figure 3.2a) the 48-hour survival rate remained relatively constant throughout the experiment at each density, while in the dry season experiments (Figures 3.2b and 3.2c) the 48-hour survival rate declined through time.

3.3.2.2 Patterns of Growth.

Although most metamorphs demonstrated growth but not a distinct change from stage 2 to stage 3, some metamorphs at Calvert Hills during the wet season did demonstrate this change.

The main effects of experiment (season and region) and density on total growth were significant (Table 3.4). The experiment by density interaction however, was not significant. This shows that total metamorph growth (to day 14) differed between experiments and that within experiments growth was affected by the density of metamorphs.

The analysis of daily differences in size (Table 3.4) indicates that the time by experiment, time by density and time by experiment by density interactions, significantly affected metamorph growth rates. The 48-hour growth of metamorphs was therefore affected by combinations of the effects of experiment (season confounded with region) and

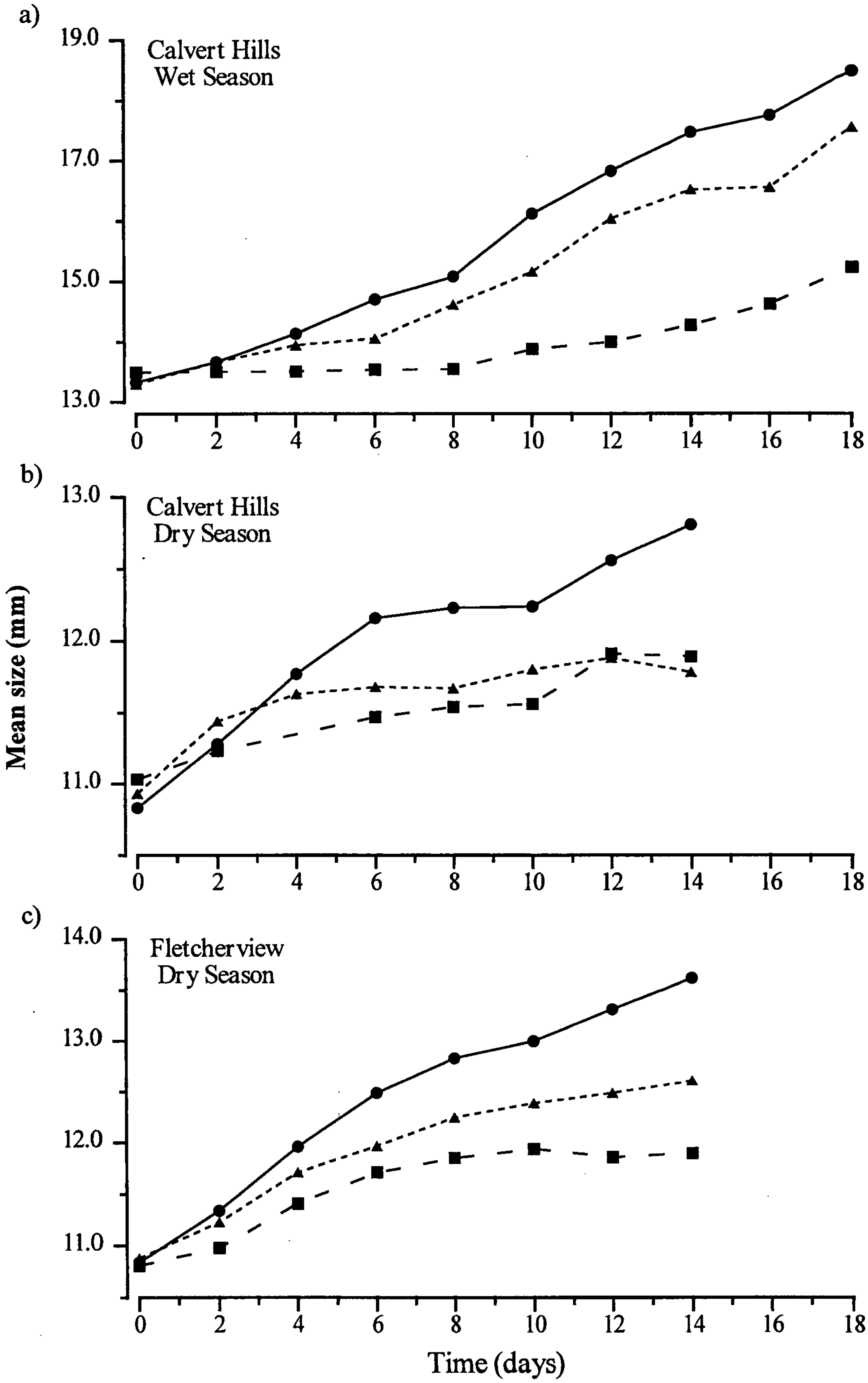
density of metamorphs within the enclosures, and the strength of these effects varied over time within experiments (Figure 3.3).

Table 3.4. Profile analysis of growth rates of metamorphs in the enclosure experiments. The analysis of totals examines cumulative growth over the period of the experiment. The analysis of differences examines the shape of the curves of size against time in each treatment. (* = significant at 0.05 level).

	Mean Square	Wilkes' λ	d.f.	F	*P*
Analysis of Totals (ANOVA)					
Experiment	206.4		2	168.17	0.0001*
Density	17.37		2	14.15	0.0001*
Experiment*Density	1.65		4	1.34	0.2824
Error	1.23		24		-
Analysis of Differences (MANOVA)					
Time		0.04	718	69.33	0.0001*
Time*Experiment		0.03	1436	11.28	0.0001*
Time*Density		0.11	1436	5.03	0.0001*
Time*Experiment*Density		0.07	2866	2.61	0.0007*

Figure 3.3. Mean metamorph size in experimental enclosures at initial densities of 3.3 m^{-2} (●, solid line), 6.7 m^{-2} (▲, short dashed line), and 16.7 m^{-2} (■, long dashed line).

a) Calvert Hills, in January-February 1988;
b) Calvert Hills, April-May 1988;
c) Fletcherview, June 1989.


a)
19.0
17.0
15.0
13.0
Calvert Hills
Wet Season
0
2
4
6
8
10
12
14
16
18
b)
13.0
12.0
11.0
Calvert Hills
Dry Season
0
2
4
6
8
10
12
14
16
18
c)
14.0
13.0
12.0
11.0
Fletcherview
Dry Season
0
2
4
6
8
10
12
14
16
18
Mean size (mm)
Time (days)

For all densities combined, total growth was greatest in the Calvert Hills wet season experiment (Figure 3.3a) and least in the Calvert Hills dry season experiment (Figure 3.3b). In all three experiments, the total growth of animals was greatest at a density of $3.3/m^2$ (Figure 3.3). Figure 3.3 also suggests the source of the significant interaction effects found in the profile analysis with patterns of change in size between measurements differing among experiments. In the Calvert Hills wet season (Figure 3.3a), the curves of size against time are upwardly concave, suggesting that the instantaneous growth rate was relatively constant through time. In the dry season experiments (Figures 3.3b and 3.3c) the curves are concave downward, suggesting that instantaneous growth rate decreased through time.

3.3.3 Correlations with the Biotic and Abiotic Environment.

For all experiments combined, the number of surviving metamorphs is significantly negatively correlated with the percent size increase/48-hours, but not with the percent surviving/48-hours (Table 3.5). Metamorph growth rate was therefore density-dependent with growth rates increasing as density decreased. Metamorph survival rate was not affected by the number of surviving metamorphs present in the enclosures.

Table 3.5. Spearman's coefficients of rank correlation of 2-day growth increments and survival rates with density and environmental factors. (*$P<0.05$; **$P<0.01$; ***$P<0.001$)

Experiment	Response	Density	Temperature		Rainfall
			Maximum	Minimum	
All Combined	**Growth Rate**	-0.35***	-0.01	0.11	-[a]
	Survival Rate	0	-0.24**	-0.15*	-[a]
Calvert Hills, Wet Season	**Growth Rate**	-0.57***	-0.17	-0.22*	-0.01
	Survival Rate	-0.16	0.1	0.02	0.15
Calvert Hills, Dry Season	**Growth Rate**	-0.06	0.06	-0.07	-[b]
	Survival Rate	0.01	0.12	0	-[b]
Fletcherview	**Growth Rate**	-0.23	-0.02	0.26**	0.13
	Survival Rate	-0.02	-0.25*	0.35***	0.11

[a] = Not calculated.

[b] = No rain during the sample period.

In the separate analyses of each experiment (Table 3.5), rainfall did not significantly affected growth or survival. The effects of temperature and density differed among experiments. The variation in results is probably due to the climatic and seasonal differences between the two Calvert Hills samples and the Fletcherview sample. In the Calvert Hills wet season experiment, metamorphs grew rapidly, and temperatures fluctuated markedly both within and between days (daily maximum: $\bar{x}$ = 35°, range 28-40°; daily minimum: $\bar{x}$ = 25°, range 21-26°). Maximum and minimum temperatures were both negatively correlated with metamorph survival rates. In the dry season experiment at Calvert Hills, metamorphs grew very slowly, while maximum and minimum temperatures varied less than in the wet season (daily maximum: $\bar{x}$ = 34°, range 29-37°; daily minimum:

$\bar{x}$ = 19°, range 15-21°). There was thus less variation in either the dependent or independent variables in the analyses, and any correlations were probably obscured by random variation. Temperatures were lower during the Fletcherview dry season experiment (daily maximum: $\bar{x}$ = 25°, range 24-28°; daily minimum: $\bar{x}$ = 17°, range 15-17°). It appears that at these low temperatures, rates of growth and survival increase as minimum temperature increases, but survival decreases with increasing maximum temperature.

The correlation of the difference between maximum and minimum temperature (an index of relative cloud cover) with the entire daily survival rate data showed a significant negative effect on the 48-hour percentage survival of metamorphs. That is, as the difference between maximum and minimum temperatures decreased, the daily survival rate of metamorphs increased.

3.3.4 Growth and Survival to Juvenile Size.

Daily growth rate was significantly associated with the index of total biomass/m^2 in the two experiments (Table 3.6). The third experiment however, was not significant, but as it was suggestively close, it led to a simulation that was a good fit to the data. The simulations of growth and survival to 30 mm SVL (Table 3.6) indicate that when the initial density is 3.3/m^2, 1.3 to 1.5 and 2.0 to 3.4 times as many animals would survive to juvenile size than would survive when the initial density is 6.7 or 16.7/m^2, respectively. The models also indicate that the time taken to grow from 10 mm SVL to 30 mm SVL could vary from 50 days at an initial density of 3.3/m^2 in the wet season, to 138 days at a initial density of 16.7/m^2 in the dry season at Fletcherview.

Table 3.6. Mean survival rates, regression models for daily growth rate, and predicted time and survival from 10 to 30mm SVL for each experiment and density.

(g = proportion increase in SVL day^{-1}; b = index of biomass m^{-2}, estimated as $\sum[(\mathrm{SVL}/10)^3]$)

Density (Individuals m $^{-2}$)	Days to 30mm SVL	Percentage Survival to 30mm SVL
Calvert Hills, Wet Season		
Daily survival rate, $\bar{x} = 0.9326$		
$g = 1.0241e^{-0.000695b}$; $r = 0.44$; $P<0.001$		
3.3	50 (n = 50)	3.05
6.7	54 (n = 100)	2.31
16.7	62 (n = 250)	1.32
Calvert Hills, Dry Season		
Daily survival rate, $\bar{x} = 0.9569$		
$g = 1.0115e^{-0.000294b}$; $r = 0.21$; $P = 0.1256$		
3.3	101 (n = 50)	1.16
6.7	106 (n = 100)	0.93
16.7	117 (n = 250)	0.57
Fletcherview, Dry Season		
Daily survival rate, $\bar{x} = 0.9788$		
$g = 1.0173e^{-0.000430b}$; $r = 0.32$; $P = 0.0011$		
3.3	81 (n = 50)	17.64
6.7	100 (n = 100)	11.74
16.7	138 (n = 250)	5.2

3.4 Discussion.

Newly metamorphosed toads spend their first terrestrial weeks near water (Boomsma and Arntzen 1985). This dispersal delay may be due to small toads undergoing post-metamorphic physiological changes such as rapid increases in oxygen transport capacity (Pough and Kamel 1984), and a decrease in area/volume ratio which decreases relative rates of evaporative water loss. The time in which metamorphs remain near water is also a period of heavy mortality (Licht 1974). Metamorphs are vulnerable to the physical environment, predators and competitors (Freeland and Kerin 1991).

Most of the metamorphs in this study were located within 1 m of water, with the smallest class (stage 1), found almost nowhere else. Freeland and Kerin (1991) also found more metamorphs at the water's edge than at five metres from the water. The spatial distribution of metamorphs may be caused by stage-specific movement behaviour, but may also in part reflect very slow diffusion away from water. Using simple simulations, which showed that biased random movement at a net rate of 5cm/day away from water during the wet season and 2 cm/day in the dry season, produced spatial distributions similar, but not identical, to those observed.

It is likely that the stage-specific pattern of dispersal is not entirely due to diffusion. The difference between the spatial distributions of stage 3 and 4 metamorphs in the wet season, and the similarity between their distributions in the dry season, are both greater than would be expected if metamorphs were simply diffusing slowly away from water. Richards and Lehman (1980) proposed that day length and ambient temperatures may strongly affect behaviour during the early stages of post-metamorphic development. During the wet season sampling period, diurnal air temperatures were extreme (up to 45° C). At these times smaller metamorphs were concentrated at the water's edge, presumably to avoid

desiccation. During these periods it is likely that only the larger stage 4 metamorphs could withstand being away from the water's edge.

Freeland and Kerin (1991) also demonstrated that larger metamorphs dispersed farther from water. Stage 4 metamorphs in this study may have been foraging where there were fewer toads or exploiting less crowded retreat sites. In contrast to the wet season, diurnal dry season temperatures were lower. During this time, only smaller metamorphs (stages 1 and 2) remained close to the water, while larger individuals (stages 3 and 4) were more evenly distributed away from the water's edge. The effects of these patterns do not depend on whether they are caused by stage-specific behaviour or diffusion. In either case, the close proximity to water of small metamorphs would prevent dehydration and increase evaporative cooling during the day, and the greater dispersal of larger metamorphs would provide less crowded conditions.

The highest mortality rate in terrestrial amphibians is likely to occur during the period on land immediately after metamorphosis. It has been suggested that *B. marinus* lose their larval toxicity at metamorphosis and do not regain it until juvenile size is attained (Zug and Zug 1979). Lower toxicity might increase the risk of predation between metamorphosis and 30mm SVL. The predators of *B. marinus* metamorphs, however, are not well known. Metamorph activity is highest during the day, exposing them to diurnal predators (Freeland and Kerin 1991). Zug and Zug (1979) suggested that many mammals, birds, reptiles and amphibians, including adult *B. marinus*, eat metamorphs and juveniles. Wolf spiders (family Lycosidae) were observed during this study preying on small metamorphs. Ants (*Iridomyrmex purpurea*) have also been observed preying heavily on metamorphs as they emerge from ponds.

Mortality rates of post-metamorphic amphibians can be affected by environmental factors such as temperature and precipitation (Berven 1990). Pond-drying and hydro period

may also affect the survival rates of post-metamorphic toads (Pechmann *et al.* 1989; Semlitsch and Wilbur 1988).

In the enclosure experiment there was a significant effect of experiment on total metamorph survival. Daily survival rates were greatest at Fletcherview in the dry season, and worst at Calvert Hills in the wet season (Table 3.6). These experimental effects were a combination of season and site differences among experiments. The seasonal differences were caused by the timing of each experiment; wet season for experiment 1, early dry season for experiments 2 and 3. High temperatures, large variations between maximum and minimum temperatures, and extreme diurnal maximum temperatures are characteristic of the wet season, while early dry season temperatures are lower and usually more stable, with less variation between maximum and minimum temperatures. The site differences may have been caused by differences in temperature and humidity, and may also have been due to differences in the substrate, ground cover, available prey, and predator fauna between the regions.

In addition to environmental effects, survival rates of metamorphs may respond to density. Pearson (1955, 1957) demonstrated that monthly survival rates of spadefoot toads in enclosed populations were highest at intermediate densities. The daily survival rate in the enclosure experiment, however, did not depend on density. While density did not affect daily survival rate, seasonal and environmental factors did. For instance, the percent of metamorphs surviving/48-hour decreased significantly at high maximum temperatures. This suggested that metamorph survival is affected by the amount of cloud cover. To examine these results further, correlations of daily survival with the differences between maximum and minimum temperatures, described as an index of relative cloud cover (R. Alford; personal communication) were performed. These showed that temperature difference had a significant negative effect on 48-hour percent survival and growth rate thus suggesting that cloud cover increases survival.

Mortality rates of post-metamorphic amphibians may be constant with age (Turner 1960), or may decrease with increasing size or age (Clarke 1977; Claussen and Layne 1983; Berven 1990). In the current study, mortality rates in two of three experiments increased slightly through time.

The strongest increase was at Fletcherview in the dry season, and the correlation analysis (Table 3.5) suggests that this was probably caused by changes in the physical environment, rather than changes in metamorph size or age. The most parsimonious interpretation of these data appears to be that mortality rates are relatively constant over at least the first 14-18 days following metamorphosis.

Growth rates in this study were significantly negatively related to density. Pearson (1955) suggested that decreased growth at higher metamorph densities was probably due to a lesser food supply per individual. Such competition might explain these results, but other factors such as increased physiological stress caused by limited availability of good retreat sites may also have been responsible for the results.

The simulated survival and growth predictions of metamorphs were highest at densities closest to those calculated in the field (Table 3.6). Higher densities reduced a metamorph's rate of growth and therefore reduced its survival chances. However, these higher densities were not noted in the field (Table 3.1). This result implies that the number of tadpoles simultaneously emerging from their natal pool may reach a carrying capacity.

The results from this chapter indicate that the fewer number of metamorphs emerging from a single pool then the higher the growth and therefore survival rates through to juvenile size (30mm). *B. marinus* may therefore be able to adust the number of tadpoles metamorphosing simultaneously. This could be achieved by competition between tadpoles of the same age and size reducing growth and survival rates and/or by having a reasonably

prolonged breeding season. Both of these life history traits have previously been demonstrated.

Despite laying large egg clutches, Hearnden (1991) showed in his study on *B. marinus* tadpoles, that density-dependence of tadpole growth and survival limited the number of tadpoles metamorphosing at the same time. Furthermore, the breeding season of *B. marinus* in the wet/dry tropics has been documented as continuous throughout the wet season with isolated breeding events late in the dry season (Zug and Zug 1979; Freeland 1984; Hearnden 1991). A prolonged breeding season, as opposed to a short breeding burst, suggests that tadpole metamorphosis, and the subsequent congregation of newly emerged metamorphs, will be at a steady rate over a protracted period thus reducing density and growth pressures of metamorphs.

3.5 Summary.

B. marinus metamorphs emerge from water at very small sizes and congregate around the edge of their natal pool. During this time their survival rates are more influenced by environmental factors rather than density. Although daily mortality rates were not affected by density, the lower growth rates experienced by *B. marinus* metamorphs at higher densities would prolong the time spent as metamorphs, exposing them greater cummulative risk. However, as mortality from environmental factors reduces density, metamorph growth rates increase. A change in activity patterns usually follows increasing growth rate with metamorphs venturing further from the water's edge. The reduced density away from the water and increased growth opportunities (ie. more available food), allows toads to rapidly increase their growth and therefore maximise their survival potential. The ability to rapidly achieve greater size also allows toads to better cope with harsh environmental extremes therefore increasing their chances of survival through to larger stages.

When combined with varying activity patterns away from the water's edge, the density-dependent growth rates and density-independent daily survival rates of metamorph *B. marinus* lead to density-dependent cummulative survival to the 30 mm juvenile size. This survival and growth strategy may have implications on the number and timing of *B. marinus* metamorphosis and the duration of the adult breeding period.

Chapter 4. Toad Growth.

Abstract

Change in body length over time of recaptured toads were used to calculate growth rates for Calvert Hills and Townsville populations. The growth rates of *B. marinus* (≥30mm) are reported for exotic populations and are shown to be faster than previously reported for endemic populations of *B. marinus* and other species of *Bufo*. Toads at Calvert Hills took half the time to reached adult size of 90mm than at Townsville. Once this size was achieved, growth rates slowed considerably at both locations despite the asymptotic length of each population being similar. Although growth rates were similar between locations during the dry season, toads displayed higher growth rates, combined with an increase in body condition, during the wet season at Calvert Hills. This period of higher growth rates and increased body condition at Calvert Hills corresponded with high temperatures and peak food supplies. *B. marinus* is a typical ectotherm and the higher growth at Calvert Hills during the wet season is probably primarily due to the higher temperature regime experienced at this location during this season. Differences in growth rates between the two locations may also be caused by density-dependant effects at Townsville (higher number of toads active at sites leading to lower growth rates). Higher growth rates at Calvert Hills indicated that adult toads could potentially breed within a year of emergence onto land. The growth curves indicate that Townsville toads do not attain adult size until their second year and females probably compensate for slower growth by breeding at smaller sizes.

4.1 Introduction.

A typical growth pattern of anurans includes an asymptotic growth curve with a steep slope up to maturity, with continued growth thereafter at a decreased rate (Gibbons and McCarthy 1984; Ryser 1988). The von Bertalanffy growth equation has previously been used to demonstrate amphibian growth because it best suits animals that exhibit early, rapid growth increases approaching an asymptote (Breden 1988; Hemelaar 1988). This rapid growth to maturity allows them to pass quickly through the stage with the greatest mortality (Clarke 1974), and probably enables a faster attainment of reproductive status (Ryser 1988). The average growth rate of individuals within a population typically slows as they mature and this may be due to either direct effects of age or changes in size itself (Kirkpatrick 1984).

Within a population many individual animals exhibit large variations in growth. This leads to variations in age-specific sizes, seasonal growth within and between populations of the same species. One of the primary reasons for such variations is changes in temperature and moisture. Climatological factors often exert influences on population characteristics, including growth rates (Hemelaar 1988). Variation in size-specific growth results from environmental influences and relates to variation in food intake and/or microclimate (Ryser 1988). Most of the studies on amphibian growth have been performed during periods of high activity such as the breeding season. However, few studies have attempted to make comparative studies of amphibian populations outside their breeding season (Denton and Beebee 1993a). For instance, tropical habitats, with distinct wet and dry seasons, may exert seasonal effects on amphibians causing marked variation in foraging activity and consequently changes in growth (Halliday and Verrell 1988; Gallati 1992).

In addition to environmental factors, comparative growth rates from toad populations may show considerable variation due to resource stresses at high population

densities. For example, at high densities *Bufo calamita* grew relatively more slowly from metamorphosis onward, and maintained these low growth rates into old age. Furthermore, individual variation in growth rates was highest in high-density populations and was attributed to increased competition for food and/or the most favourable microhabitat (Denton and Beebee 1993a).

Except for a relatively small-scale study within their native range (Zug and Zug 1979), and two studies on metamorph growth (Cohen and Alford 1993; James 1994), little information is available on growth rates of *B. marinus.* It appears that toad growth patterns follow patterns of insect abundance, their major food source, growing early in the wet season with minimum growth during the dry season (Zug and Zug 1979). In their native range, *B. marinus* show a rapid increase after metamorphosis reaching 95mm approximately 420 days after emergence onto land (Zug and Zug 1979). Growth then slows reaching an asymptotic length of approximately 115mm after two years. Once having attained a size of approximately 100mm, most toads demonstrated slower growth rates with some larger toads exhibiting little or no growth at all.

The growth rates of *B. marinus* from populations in the Townsville region and those at Calvert Hills in the Gulf of Carpentaria are examined within this chapter. Using long-term mark-recapture data growth curves are generated for each population and, using data from Chapter 3 on toads less than 30mm in length, a predictive table of time taken to reach various sizes and age classes is generated. Furthermore, the time taken to attain maturity and the effects of the tropical wet and dry seasons on toad growth are also examined and compared between populations.

4.2 Methods.

4.2.1 Census Technique.

Toad populations were surveyed at two sites at Calvert Hills (section 2.1.1) and three sites at Townsville (section 2.2.2) between November 1986 and January 1993. River transects were 100 metres in length with the total area covered being 1000 m^2, while transects around each dam varied according to the water level so the area sampled was equivalent to a 10 x 100 metre transect (Figure 4.1). Bell's Dam dried up after March 1992 and was not refilled. The site was therefore not used for the study after this time.

Using a spotlight or torch, visual censuses were conducted over a one hour period, commencing approximately one hour after sunset. This time represents a period when the greatest number of toads have previously been shown to be active (Zug and Zug 1979). One sample is equivalent to one nightly census, while two or more samples within a trip during a season were used to calculate population estimates. All toads encountered that were greater than 30mm in length, (the size which *B. marinus* is classified as a juvenile recruit, see Chapter 3), within river transects at Calvert Hills, (Big Calvert River and Homestead), and circumnavigation of small dams at Townsville, (Bentley Lagoon, Rock Road Dam and Bell's Dam), within an area 10 metres wide to the water's edge, were collected. Toads below 30mm SVL were difficult to detect and population characteristics of these smaller-sized toads were examined separately (see Chapter 3).

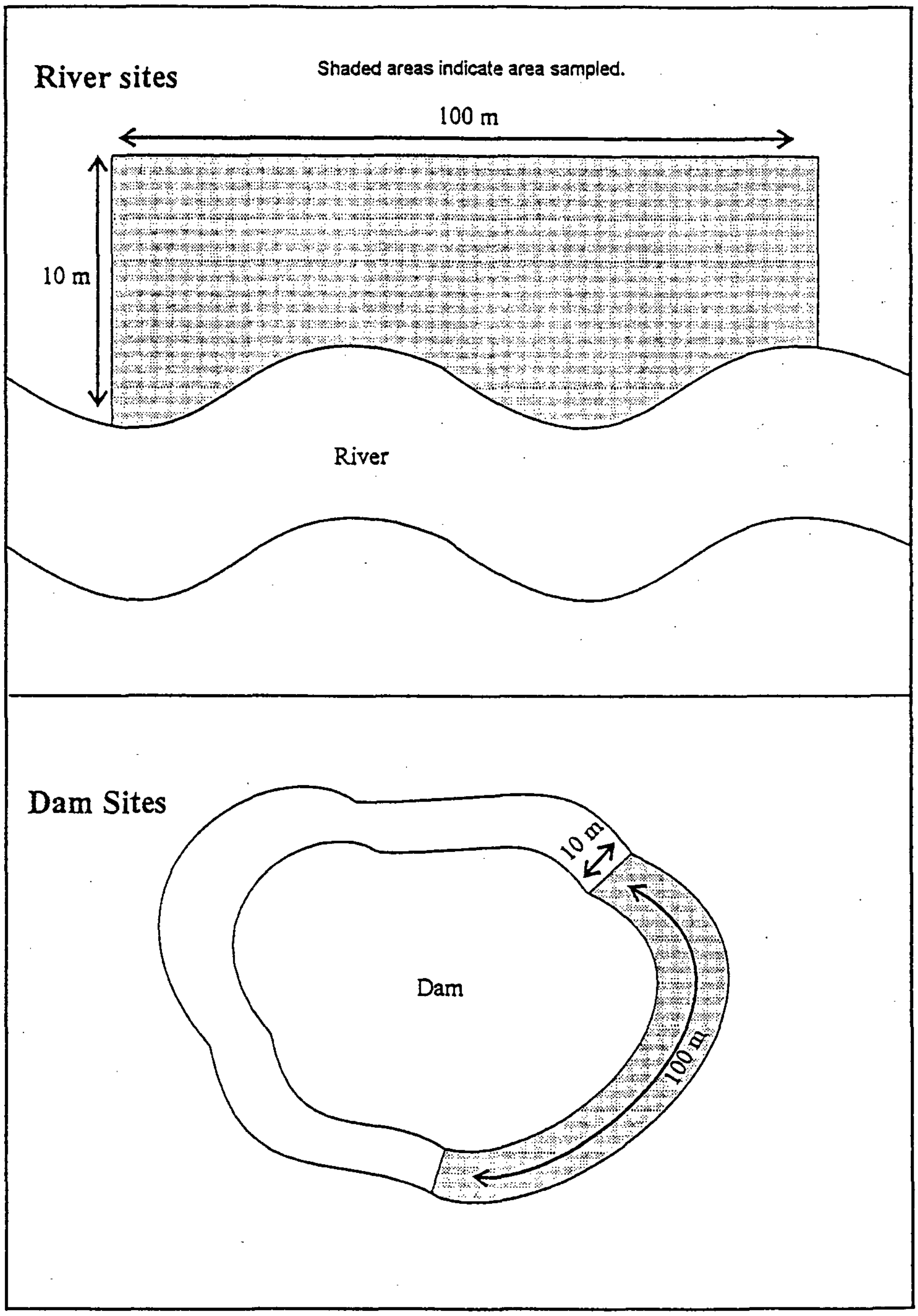


Figure 4.1. Diagram demonstrating area sampled around dam and river sites.

4.2.2 Toad Data.

Only toads with a snout-vent length (SVL) of ≥90mm can be positively sexed based on external morphology (Zug and Zug 1979; Cohen and Alford 1993; Alford *et al.* 1995). Toads ≥90mm SVL were therefore classed as adults in this study. Toads between 60 and 89mm SVL were classed as sub-adults, and those between 30 and 59mm SVL were classed as juveniles. The division between sub-adults and juveniles was made because some individuals may be sexually mature and potentially able to breed at sizes as low as 65mm SVL (Alford *et al.* 1995). However, because fecundity increases rapidly with body size, the contribution of sub-adult toads to the total reproductive output of populations is most likely negligible (Alford *et al.* 1995).

Adults were sexed based on dorsal skin texture (Straughan 1966). Males have rougher skin characterised by spinose tubercules (Tyler 1975), while females have smoother skin (less pronounced tubercules), and a similar ventral pattern to that of sub-adults and juveniles (Zug *et al.* 1975). In addition, male toads can be distinguished from females by presence of vocal sacs (Tyler 1975).

4.2.3 Marking.

The SVL for each toad was measured and the weight of each toad (to nearest 0.5 gram) was determined using either an electronic or spring balance. The weight of each toad was generally taken before the toad voided the contents of its bladder (see Chapter 6). Any unusual characteristic of individual toads was noted. Toads were individually marked using a toe-clipping system modified from Martof (1953) (Figure 4.2). This technique of toe-clipping led to no more than two toes being removed from each limb. Toes were

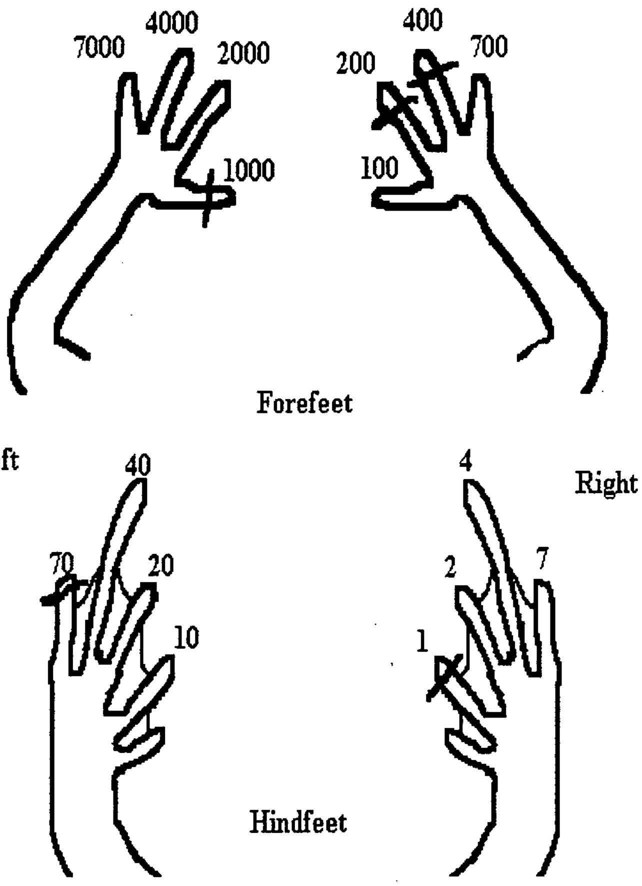


Figure 4.2. Illustration of the numbering system for toe-clipping of *B. marinus* during this study (modified from Martof 1953). For example, the first toe on the left fore leg, second and third toes on the right fore leg, fifth toe on the left hind leg and second toe on the right hind leg gave a mark of 1671.

usually clipped at the second joint except for the interior front digit (the 1000 and 100 toes) which were clipped at the first joint to minimise effects to the toad because of their relatively large size and their use by males in grasping females in amplexus. This method of toe-clipping had no detectable effect on toad survival (Alford *et al.* 1995). Recaptured toads had their number recorded and all captured toads were released at the central point of the transect immediately after processing.

4.2.4 Growth Rates.

Toad growth rates from Calvert Hills and Townsville populations were calculated from recaptured toads from a period greater than 50 days from their most previous capture. Data from recaptured toads in a time period less than 50 days were considered to be too small for toads to demonstrate any realistic growth. In addition, few capture records were obtained after a period of one year. Year to year variations in growth rates were therefore unable to be accurately calculated. As female recapture numbers were small, male and female toads were combined and analysed together.

The change in snout-vent length (ΔL) and change in time (Δt) between captures were recorded. The mid-length was calculated by adding the length at first capture to the length at recapture and dividing this value by two. The specific growth rate (SGR) of toads was then calculated as:

$$\mathbf{SGR = (\Delta L/\Delta t) /Mid\text{-}length;}$$

The relationships between SGR and reciprocal length, 1/midlength, (used as it gave the highest correlation; see Kaufmann 1981) for both Calvert Hills and Townsville were graphed, and von Bertalanffy growth equations and associated 95% confidence limits were calculated and displayed for each location.

The growth equations and curves were calculated from a minimum size of 30mm (ie. t = 30), as this was the size of the first stage of juvenile toads. The growth rates of toads <30mm, ie. metamorphs, were calculated separately and presented in Chapter 3.

From the growth curves the time for toads to reach sizes that represent different age categories (ie. time taken for 30mm juvenile toads to grow into 60mm sub-adult toads, 60mm sub-adults to grow into 90mm adults, and 90mm adults to grow to their asymptotic length), were calculated for Calvert Hills and Townsville. Data from Table 3.6 (Chapter 3) on metamorph growth rates at Calvert Hills was included.

4.2.5 Seasonal Effects.

To examine the seasonal effect on growth, all recaptured toads between 50 and 150 days at both locations, were divided into wet and dry season samples depending on the time of recapture. The 150 day time period of recaptured toads was selected so that the growth period would not encompass more than two successive seasons. That is, toads used in the analysis were originally caught during one particular season (eg. dry season) and then recaptured in the subsequent season (eg. wet season). Toads recaptured in the middle-wet and late-wet/early-dry season (the two wettest divisions; see Table 2.1) were classified as wet season samples and toads recaptured in the middle-dry, late-dry and early-wet season (the three driest divisions; see Table 2.1) were classified as dry season samples. It was

important that growth data did not encompass more than two successive seasons for this analysis to keep growth changes between the wet and dry seasons as accurate as possible.

In a further analysis toads were separated on the basis of whether they demonstrated zero or positive growth during these seasonal periods. To determine if the distributions of toad growth rate varied significantly between the wet and dry seasons, the data were then analysed with a chi-squared homogeneity test.

Specific growth rates and mean body condition index (BCI) for toads recaptured between 50-150 days during the wet and dry season samples were also each examined by a one-way ANOVA.

4.3 Results.

4.3.1 Regression Lines for Specific Growth Rates.

The relationship between SGR and reciprocal size was significant at Calvert Hills (Table 4.1, Figure 4.3a) and Townsville (Table 4.2, Figure 4.3b). At Calvert Hills the SGR = 0.51377 x Reciprocal length - 0.00411 (Table 4.1), while at Townsville the SGR = 0.22931 x Reciprocal length - 0.00181 (Table 4.2). Details of the regression analysis, including 95% confidence limits, are shown in Appendix 4.

Figure 4.3. Relationship of recaptured toads specific growth rate and the reciprocal of their size.

a) Calvert Hills;
b) Townsville.

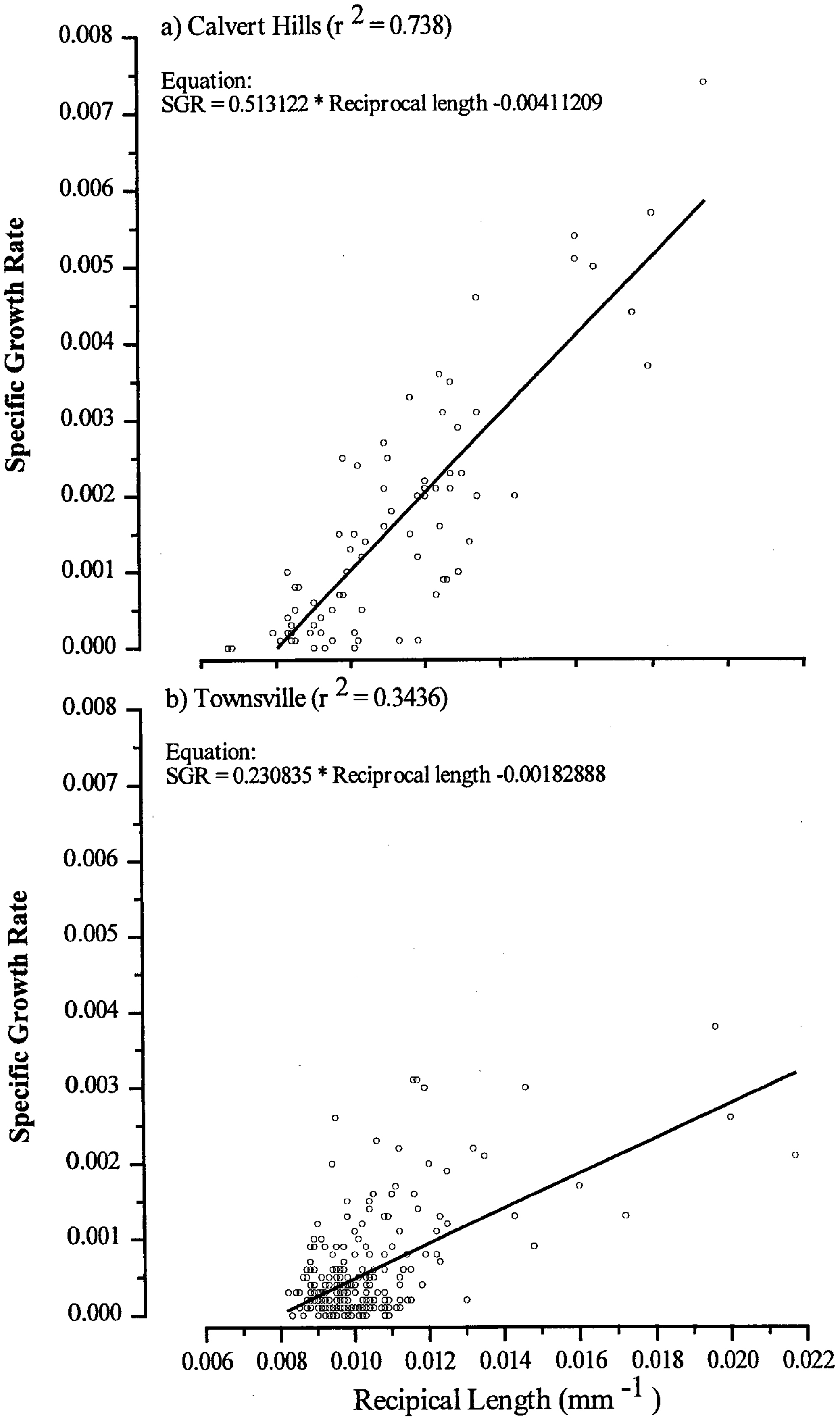

a) Calvert Hills ($r^2 = 0.738$)
Equation:
SGR = 0.513122 * Reciprocal length -0.00411209
b) Townsville ($r^2 = 0.3436$)
Equation:
SGR = 0.230835 * Reciprocal length -0.00182888
Specific Growth Rate
Specific Growth Rate
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
0.006
0.008
0.010
0.012
0.014
0.016
0.018
0.020
0.022
Recipical Length (mm^{-1})

Table 4.1 ANOVA of regression results for Calvert Hills. (* = significant at 0.05 level).

	d.f.	M.S.	F	*P*	r^2
Regression	1	1.459×10^{-4}	219.76	<0.00001*	0.738
Residual	78	6.639×10^{-7}	-	-	-

Table 4.2. ANOVA of regression results for Townsville. (* = significant at 0.05 level).

	d.f.	M.S.	F	*P*	r^2
Regression	1	3.695×10^{-5}	129.3	<0.00001*	0.3436
Residual	247	7.058×10^{-5}	-	-	-

4.3.1.1 Calvert Hills Specific Growth Rate Equation.

The following equations were calculated using the methods described by Kaufmann (1981).

The specific growth rate (von Bertalanffy) equation for toads at Calvert Hills has the following form:

$S = S\infty[1\text{-Exp-}g(t+t_0)]$; where S = size as a function of time (t).

From the previous regression (Figure 4.3a):

$S\infty$, (or the asymptotic length) = reciprocal length divided by the y intercept,
= 0.51377/-0.00411;
= 125.00mm.

t = 30, ie. metamorphs turn into juvenile toads;
t_0 = the natural log of (1 - t/asymptotic length)/g, where g = y intercept;
$t_0 = \ln (1 - 30/125)/-0.00411 = 66.77$.

The equation therefore becomes:

$$\mathbf{S = 125 [1 - Exp - 0.00411 (t + 66.77)]}$$

4.3.1.2 Townsville Specific Growth Rate Equation.

The Townsville specific growth rate (von Bertalanffy) equation for toads has the following form:

$S = S\infty[1\text{-}Exp\text{-}g(t+t_0)]$; where S = size as a function of time (t).

From the previous regression (Figure 4.3b):

$S\infty$, (or the asymptotic length) = reciprocal length divided by the y intercept,
= 0.22931/-0.00181;
= 126.70mm.

$t = 30$, ie. metamorphs turn into juvenile toads;

t_0 = the natural log of (1 - t/asymptotic length)/g, where g = y intercept;

$t_0 = \ln (1 - 30/126.7)/-0.00181 = 149.23$.

The equation therefore becomes:

$$\mathbf{S = 126.7\,[\,1 - Exp - 0.00181\ (t + 149.23)]}$$

4.3.2 Rate of Growth.

The growth curves and 95% confidence limits calculated from von Bertalanffy growth equations are illustrated in Figure 4.4. The growth rate of toads varied between locations and was higher at Calvert Hills than at Townsville (Table 4.3). Juvenile toads at Calvert Hills for example, reached 60mm in 93 days, less than half that taken by juvenile toads at Townsville. Similarly, the time taken for sub-adult toads (60mm) to grow into adult toads (90mm) was approximately half (150 days at Calvert Hills v 329 days at Townsville). Furthermore, adult toads at Calvert Hills grew from 90mm to 120mm, approximately two and a half times as fast as those at Townsville. The asymptotic length of toads however, was similar at both locations (Calvert Hills = 125mm; Townsville = 126.7mm).

Figure 4.4. Von Bertalanffy growth curve and 95% confidence limits for recaptured toads.

a) Calvert Hills;
b) Townsville.

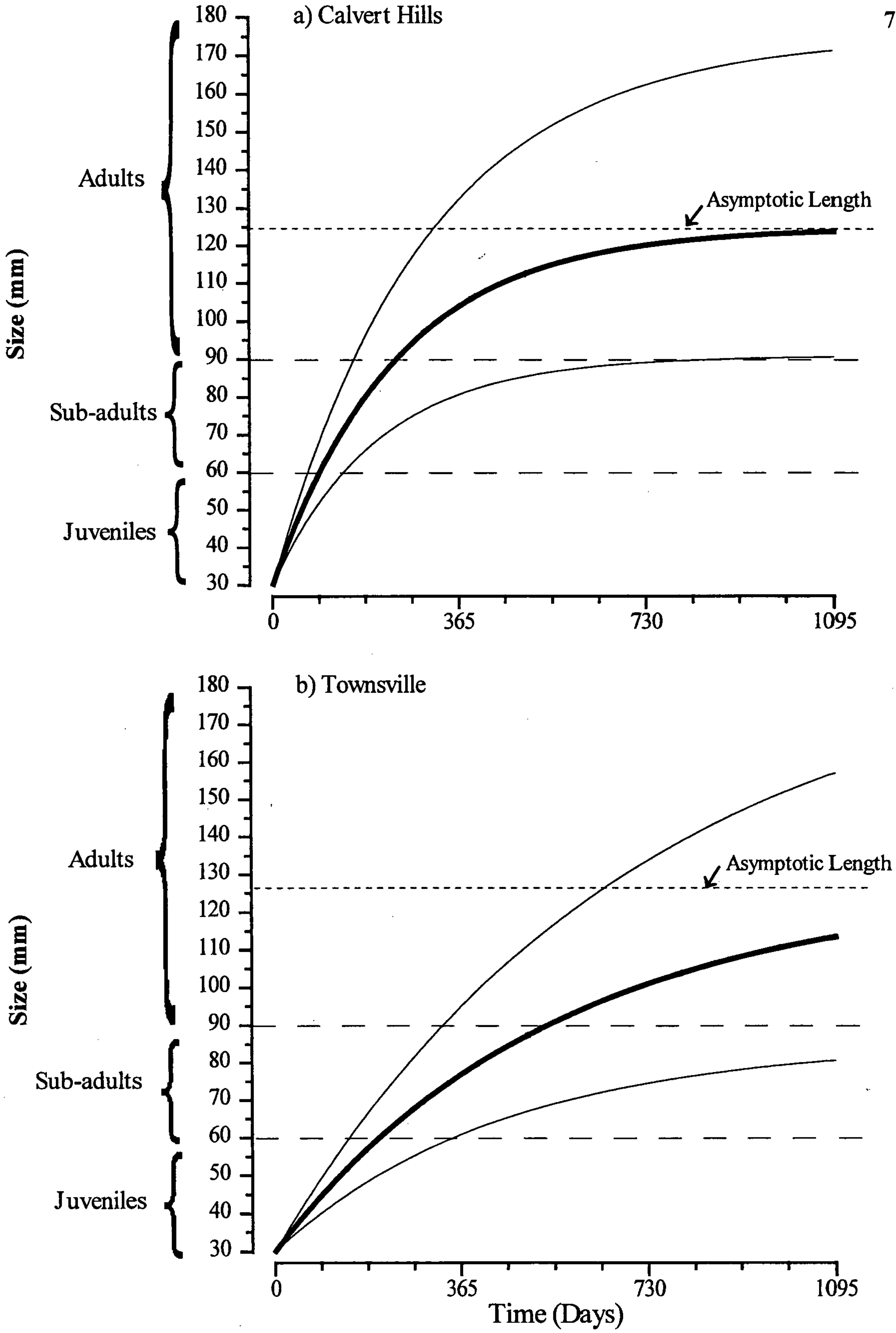

a) Calvert Hills
Size (mm)
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
Adults
Sub-adults
Juveniles
Asymptotic Length
0
365
730
1095
b) Townsville
Size (mm)
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
Adults
Sub-adults
Juveniles
Asymptotic Length
0
365
730
1095
Time (Days)

Table 4.3. Number of days and 95% confidence limits for *B. marinus* to reach 30, 60, 90 and their asymptotic length at Calvert Hills and Townsville. (* = results from density 6.7 m^{-2} at Calvert Hills, from Table 3.6; ** = results from density 6.7 m^{-2} at Fletcherview, from Table 3.6).

Size (mm)	Calvert Hills		Townsville	
	No. Days	95% Confidence Limits	No. Days	95% Confidence Limits
To 30 mm (Metamorphs)	54*	-	100**	-
30 - 60 mm (Juveniles)	93	70 - 139	206	147 - 351
60 - 90 mm (Sub-adults)	150	91 - 728	329	184 - >1000
90 - asymptotic length (Adults)	474	228 - >1000	1143	466 - >1000

4.3.3 Seasonal Effects on Growth.

There was a significant difference between the proportion of toads exhibiting either growth or no growth in the wet and dry season (Calvert Hills: Yates' corrected chi-square = 4.09; 1 d.f.; P <0.05; Townsville: Yates' corrected chi-square = 40.45; 1 d.f.; P <0.05) (Table 4.4). For both locations there was significantly higher proportions of toads exhibiting zero growth in the dry season.

Table 4.4 Number of toads recaptured between 50 and 150 days that showed positive or zero growth during the wet and dry seasons.

Season	Positive Growth		Zero Growth	
	n	%	n	%
Calvert Hills				
Wet Season Samples	31	43.1%	41	56.9%
Dry Season Samples	10	22.7%	34	77.3%
Townsville				
Wet Season Samples	79	64.2%	44	35.8%
Dry Season Samples	145	32.2%	306	67.8%

The specific growth rates of recaptured toads were also greater during the wet season compared to the dry season samples at both locations (Calvert Hills: $P < 0.05$; 1 d.f.; $F = 7.35$; Townsville: $P < 0.05$; 1 d.f.; $F = 7.26$). Mean specific growth rates during the wet and dry season at both locations are shown in Figure 4.5.

The mean body condition index or BCI (see Chapter 6) of recaptured toads was also greater during the wet season compared to the dry season samples at both locations (Calvert Hills: $P<0.05$, 1 d.f.; $F= 39.05$; Townsville: $P<0.05$; 1 d.f.; $F = 244.51$). Mean BCI during the wet and dry season at both locations are shown in Figure 4.6.

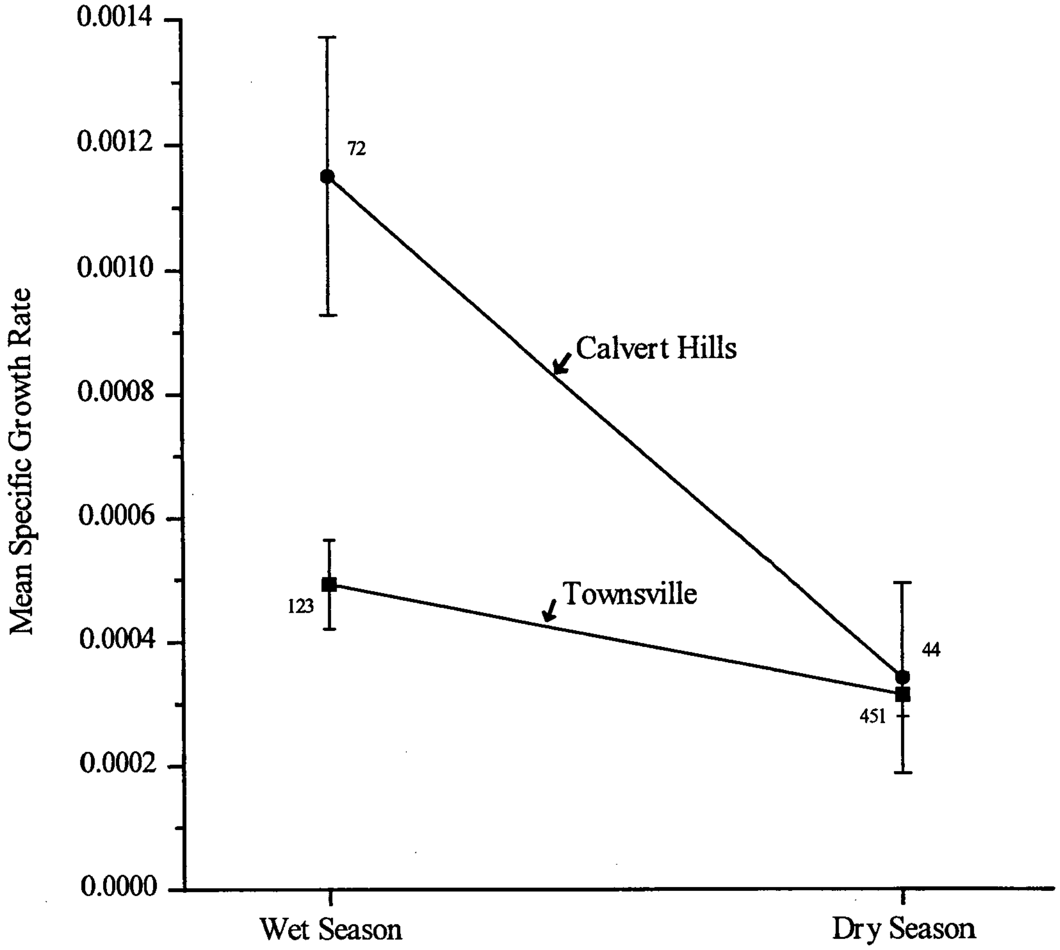


Figure 4.5. Mean specific growth rate of toads recaptured after 50 to 150 days during wet and dry season samples at Calvert Hills (●) and Townsville (■). (Standard errors are included).

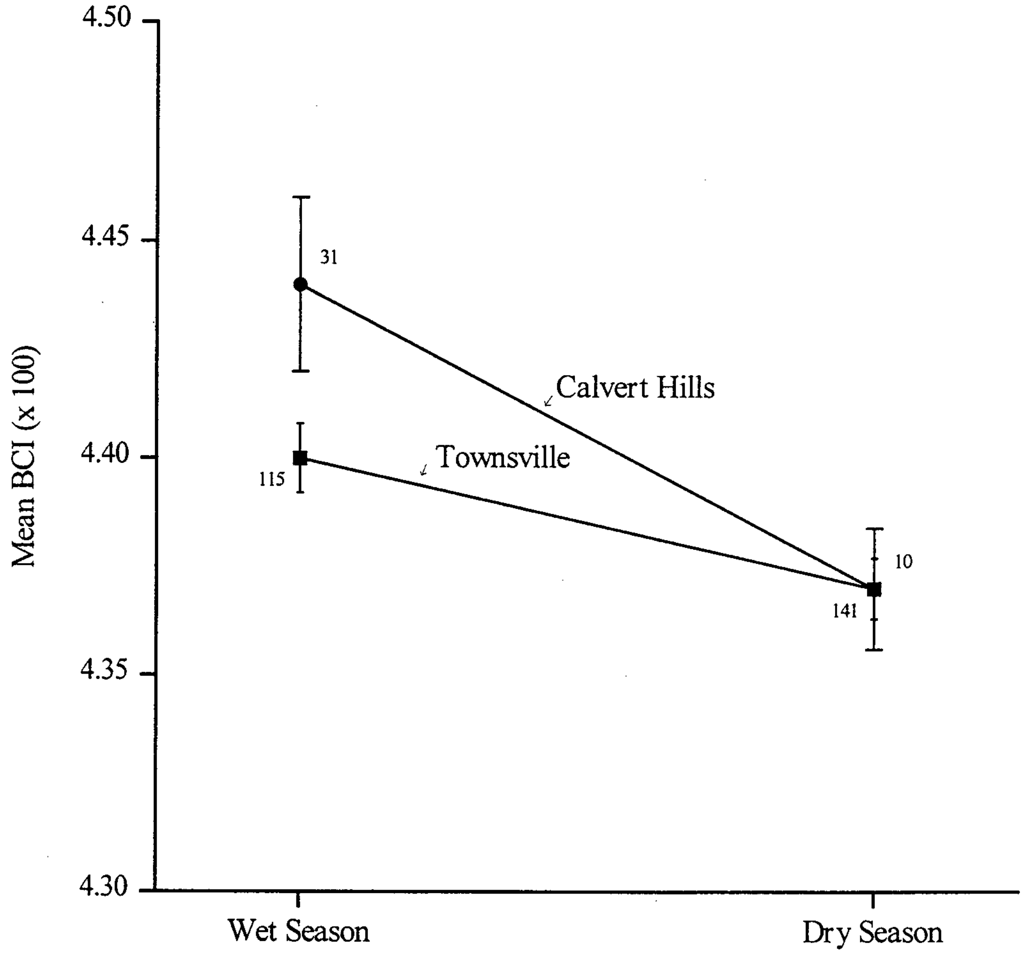


Figure 4.6. Mean body condition index (BCI) of toads recaptured after 50 to 150 days during wet and dry season samples at Calvert Hills (●) and Townsville (■). (Standard errors are included).

4.4 Discussion.

The growth curves (Figure 4.4) and calculated growth rates from Chapter 3 (Table 3.6) show that once a tadpole metamorphosed into a small terrestrial metamorph, at approximately 8mm in length, it took approximately 300 days to reach an adult-sized toad (90mm) at Calvert Hills, and over 700 days at Townsville. Once adult size was attained toad growth rates slowed considerably at both locations but adults of the same age at Calvert Hills were larger than those at Townsville. Many factors, such as climate and temperature differences between study sites, the age of toad populations, regional variation in the number of toads active, food availability, may be responsible for variations in growth rates.

The generation times calculated from the von Bertalanffy equation at Calvert Hills indicate a shorter generation time than previously reported for *B. marinus* (Zug and Zug 1979), and for other species of toads (Clark 1974; Halliday and Verrell 1988; Reading 1988; Denton and Beebee 1993a). For example, toads at Calvert Hills were shown to take less than a year to grow from first emergence from water, ie. 8mm, to a size where breeding is probable (90mm). As a result of these rapid growth rates eggs laid early in a wet season may result in potentially breeding adult toads during the following season. Shorter generation times as shown by toads at Calvert Hills are characteristic of many successful invading species (Ehrlich 1989).

The time taken for Townsville toads to reach adult size is approximately double that at Calvert Hills. Even using the best growth rates calculated from 95% confidence limits, Townsville toads still take over 400 days to achieve adult size and suggests that there is no possibility of toads at Townsville breeding in their first year. Due to slower growth rates, females breeding in their second year at Townsville will therefore be at a smaller size than same age breeding females at Calvert Hills. In addition to faster generation times, the

breeding potential of *B. marinus* populations at Calvert Hills is therefore higher than similar populations at Townsville.

The most plausible explanation for faster growth rates and generation times experienced by toads at Calvert Hills compared to those at Townsville is due to climate differences between the two regions. Growth of most ectotherms, including amphibians, are generally faster at higher temperatures. Diurnal temperatures recorded at Calvert Hills were generally higher than those at Townsville especially during the wet season (see Figure 2.4). It was during the wet season when significant differences in growth rates and body condition of toads between each location were recorded (Figures 4.5 and 4.6) with considerably higher growth and better condition of toads at Calvert Hills than at Townsville.

Due to the relatively low rate of long-term recaptures of cane toads during the study, seasonal data over several years were combined. It must therefore be recognised that differences between the quality of seasons, ie. rainfall and temperature variation between years, may have also affected growth patterns within populations of the same region and between Calvert Hills and Townsville populations. Rainfall variations between years were considerable (see Figure 6.3), while large temperature fluctuations were minimal and generally followed the pattern shown in Figure 2.4. Yearly rainfall fluctuations are therefore likely to affect the number of toads surviving through a season where low rainfall decreases survival opportunities (due to hydric stresses), and high rainfall increases survival opportunities (due to higher food supplies). However, it is unlikely that rainfall variations are primarily responsible for individual growth rates of toads. It is more probable that the higher growth rates and increased body condition experienced by Calvert Hills toads during the wet season compared to Townsville are primarily a consequence of higher temperatures.

In contrast to Calvert Hills, Townsville toad populations may be more stable but are exposed to lower temperatures and therefore show a reduced rate of growth and a lower overall body condition. In addition to leading to increased rates of growth and overall body condition, higher temperatures may also lead to more food especially during the wet season at Calvert Hills as the food supply of *B. marinus* (eg. invertebrates) are higher in seasonal environments in the wet-dry tropics during the wet season (Jansen 1973).

A higher proportion of toads at Townsville demonstrating zero growth may also have been affected by the proportion of toads that reached their asymptotic size. These toads may therefore have been limited by growth opportunities. The higher number of adults within Townsville populations, shown in Chapter 5, supports this hypothesis.

Density-dependant factors may also affect toad growth rates. For example, high density populations of *Bufo calamita* were shown to be in poorer condition and have relatively low growth rates compared to low density populations (Denton and Beebee 1993a). Their study suggested that high density toad populations suffered resource stress and therefore wandered further to seek out available food. Similar density-dependant factors may also be operating on the Townsville population, thus reducing their relative growth rates. Toad density, calculated as activity indices in Chapter 5, were generally higher around water sources at Townsville than at Calvert Hills. These density differences were possibly caused by overall site differences. For instance, Townsville sites were situated around isolated dams where toads congregated in order to rehydrate. In contrast, toads at Calvert Hills were spread along river banks thus leading to a more evenly distributed concentrations of toads. These different spacial patterns of toad numbers at each location may have an influence on growth rates. Although not tested, the amount of available food per toad may therefore have been less at Townsville compared to Calvert Hills thus leading to high density-dependant factors operating on toad growth.

4.5 Summary.

The time taken for *B. marinus* to emerge from water to reach adult breeding size was much lower for toads at Calvert Hills than at Townsville. Higher growth rates for Calvert Hills toads occurred during the wet season corresponding to a period of higher temperatures. As a result of faster growth rates, Calvert Hills toad populations could potentially breed within one year of being deposited as eggs. In contrast, Townsville toads grew slower and could not breed within their first year. Higher temperatures leading to increased food availability at Calvert Hills may also contribute to higher growth rates at this location. However, density-dependant factors may also be operating on individual toad growth within populations. For example, high numbers of toads active at isolated dam sites at Townsville may increase competition for a limited food supply and hence decrease growth rates.

Chapter 5. Population Size and Structure.

Abstract.

A long-term mark-recapture study of the number of toads active along water sources at Calvert Hills and Townsville was performed. Higher numbers of toads were active at Townsville than at Calvert Hills. This variation was due to higher numbers of active male toads. At Calvert Hills the number of sub-adult and juvenile toads peaked late in the wet season and into the early dry season. The short-term peak of non-adult toad activity probably corresponded to a shorter and perhaps more intense breeding season at Calvert Hills. Climatic variations between the two locations are presented as the main cause of seasonal activity fluctuations. The influence of rainfall and temperature variables on toad activity was also examined by a multiple regression. It was shown that toad activity is influenced by rainfall. After recent rain toads readily obtained their hydric requirements and were therefore able to forage away from water sources. However, the longer the period since rain, the higher the requirement for toads to return to a water source to rehydrate. The size of toads during the study varied between locations and during seasons. Females were larger than males while seasonal changes in sub-adult and juvenile size probably reflects growth during favourable periods and mortality during harsh periods. Larger toads were shown to generally survive through the dry season to the wet season more readily than smaller toads.

5.1 Introduction.

Anuran populations in tropical regions are faced with various seasonal conditions associated with a wet season, (when up to 80% of the annual rainfall occurs), with extremely high diurnal temperatures, and an often long dry season with little, if any, rain. As anuran breeding patterns and cycles are often influenced by rainfall (Berven 1990; Sinsch 1992), these marked changes in seasons in the wet-dry tropics can obviously have major effects on reproduction.

Anuran population size and structure may also change over time. However, changes during different seasons are not always related to one factor, such as breeding. In harsh, tropical regions, moisture, food availability and shelter sites may play an important role in regulating *B. marinus* abundance (Zug and Zug 1979; Freeland 1986a). Furthermore, the pattern of refuge use by *B. marinus* changes dramatically with season, switching from burrows close to water in the dry season to shallow depressions away from permanent water in the wet season (Carpenter and Gillingham 1987; Freeland and Kerin 1988).

Although several studies have reported the influence of various seasonal effects, including rainfall, on anuran activity and density (Pechmann *et al.* 1989; Sinsch 1992; Duellman 1995), few have investigated longer term activity patterns and/or densities, relative to marked seasonal divisions in tropical regions. Most anuran studies have concentrated on environmental effects on breeding behaviour, but limited information is available on non-breeding population activities and abundances even though breeding and non-breeding animals often spend the same amount of time in the breeding area (Christein and Taylor 1978).

One of the major influences on the activity of anuran populations is rainfall. For example, activity in *Leiopelma hamiltoni* is best accounted for by environmental factors relating to moisture, including rainfall during or preceding searches (Newman 1990). Similarly, *B. marinus* demonstrates different activity patterns during the wet and dry periods suggesting that they are strongly influenced by rainfall (van Beaurden 1978; Zug and Zug 1979). During periods of alternating dry and rainy days, rain tends to stimulate toad activity on the day of the rain and the following day, and as the number of consecutive dry days increased, the activity of the population may decline (Zug and Zug 1979). During dry periods *B. marinus* make periodic and consistent movements to waterholes presumably for rehydration, while during periods of rain they exhibit behavioural flexibility by foregoing their waterhole visits and rehydrate within their activity centres away from water (Carpenter and Gillingham 1987). Similar behaviour has been shown for the non-breeding *Rana temporaria* that are dispersed over suitable feeding grounds away from breeding ponds (Loman 1981). *Atelopus varius* also distribute themselves more uniformly during the wet season, but aggregate along rivers during the dry season for physiological reasons to prevent dehydration (Crump and Pounds 1989).

The activity of a terrestrial, nocturnal anuran is therefore best accounted for by environmental factors relating to moisture and temperature (Newman 1990) and generally occurs during the period just after dusk when toads are benefiting from high insect activity (Fitzgerald and Bider 1974). Desiccation and fluctuating body temperature are major challenges associated with the terrestrial life of amphibians (Preest and Pough 1989). In tropical regions however, temperature may not be as critical for activity and survival as it is in temperate areas. Like most members of the genus, *B. marinus* is a wide-ranging, highly mobile, ground-feeding insectivore (Freeland and Kerin 1988) that possesses an array of physiological adaptations to combat water loss (Carpenter and Gillingham 1987) such as the ability to absorb moisture from damp soil (Shoemaker *et al.* 1992), a water conserving bladder and the ability to lose up to 53% of their total body water before toads

reach a lethal limit and die (Krakauer 1970). Despite these adaptations, *B. marinus* does not possess any of the special features shown by anurans inhabiting truly arid environments such as cocoon formation and urea retention. Toad activity and abundance in the sub-tropics is therefore probably restricted by the availability of moisture (Zug and Zug 1979; Carpenter and Gillingham 1987).

In addition to hydric stresses, different age classes of toads (ie. males, females, sub-adults and juveniles) may affect the presence of other toads at a particular site. Although little has been reported on these effects on different age categories, activity patterns of adult (ie. male and female) *B. americanus* have been shown to be highly correlated (Christein and Taylor 1978), while male density and female arrival is obviously the determinant of reproductive activity (Tejedo 1992a).

The individual size of anurans also varies considerably within and among populations and is positively correlated with rainfall and food consumption that is in turn correlated to food availability (Gittens *et al.* 1980; Reading 1990; Gallatti 1992). Although age and body size are generally positively correlated, the relationship is often weak and large variation in body size can occur within a given age class (Halliday and Verrell 1988). For example, the minimum size at which *B. bufo* matures varies among populations. Minimum size when maturation occurs can vary even within populations from the same area suggesting that climatic effects are not the only factor affecting body size (Hemelaar 1988).

Notwithstanding this variation in body size between populations, female anurans are usually larger than males (Breden 1988; Reading 1990; Ritke *et al.* 1991). Despite some evidence that differences in male to female body size is driven by patterns of feeding and energy expenditure (eg. Woolbright 1983), the adaptive significance of larger female size has been assumed to be related to fecundity. Larger females often produce more and

larger eggs than small females as they potentially have more energy for reproduction (Gibbons and McCarthy 1984; Halliday and Verrell 1988; Ritke *et al.* 1991; Tejedo 1992b). *B. marinus* females are on average larger in size than males, their larger size is assumed to increase their reproductive potential (Zug and Zug 1979). Large size in female toads may, however, be disadvantageous. Gittens *et al.* (1980) suggested that the larger size of female common toads *B. bufo* might be a source of differential mortality, perhaps because they are more conspicuous to predators and/or are slower to escape from them.

In this chapter the seasonal changes and population dynamics of toad populations at Calvert Hills and in the Townsville region are described. Both these locations are associated with the wet-dry tropics of northern Australia and have marked wet and dry seasons (section 2.3.1). Furthermore, seasonal environmental effects on the population structure of *B. marinus* are examined and analysed, with relationships between toad age classes and their activity patterns at a water source investigated. Seasonal changes in body size of different age classes of *B. marinus* in tropical Australia have also been documented. This chapter therefore aims to follow and describe the differences in individual size of *B. marinus* age categories and compare populations from a relatively harsh and unpredictable wet and dry season climate of Calvert Hills to that of a more stable and predictable climate at Townsville.

5.2 Methods.

5.2.1 Census Technique and Mark-Recapture Details.

All toads were collected from an area of 1000m² (see Chapter 4, Figure 4.1) at Calvert Hills sites (Big Calvert River and Homestead) and at Townsville sites (Bentley

Lagoon, Rock Road Dam and Bell's Dam). The number of toads active per sample per trip were pooled into one of five seasonal categories (early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season; see section 2.3.1).

The methods used for a toad census, marking technique and collection of toad data such as sex, size and weight, are described in Chapter 4 (sections 4.2.1, 4.2.2 and 4.2.3). Data from these techniques is used for analysis in this chapter.

5.2.2 Seasonal Activity of Toads.

To examine the effects of season, age category and site on the number of toads active on a given sample, the data were analysed using a three-factor ANOVA. Five categories were designated to season (early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season), based on previous 30 day and following 30 day rainfall (section 2.3.1). Age categories were listed as juvenile (30-59mm), sub-adult (60 to 89mm), males and females (≥90mm). Sites at each location were Big Calvert River and Homestead at Calvert Hills Station (section 2.1.1), and Bentley Lagoon, Rock Road Dam and Bell's Dam at Townsville (section 2.2.1).

Comparisons between locations was thought to be important, but the data set were too unbalanced to enable a orthogonal nested analysis to be performed. As a consequence, the data were first analysed using ANOVA for each location separately, and, as no effect of site was found in either main factor or interactions (Appendix 5), sites were then pooled at each location and the analysis was rerun with location, age category and season as main effects. Due to unbalanced data sets, only type III sums of squares were used in the analysis. All statistical analysis was performed using SAS 6.04 (SAS Institute 1995).

To determine if the ratio of male to female toad activity varied with season, a chi-square test for heterogeneity was performed on the number of male and female toads active per sample at Calvert Hills and at Townsville for different seasons. Similarly, to determine if the ratio of adult to non-adult toad activity varied with season, a chi-square test for heterogeneity was performed on the number of adult and non-adult toads active per sample at Calvert Hills and at Townsville for different seasons.

5.2.3 Factors Affecting Toad Densities.

At each site, after nightly samples (sections 4.2.1 and 4.2.2), environmental data were recorded as follows:

a. soil temperatures were taken by inserting a thermometer into the top two centimetres of soil 10 metres from the water's edge;
b. wet and dry bulb temperatures were measured using a whirling hygrometer and % relative humidity was calculated;
c. air temperature was taken from the dry bulb reading; and
d. cloud cover was estimated as a percentage (0, 25, 50, 75, or 100%).

The values for these variables taken during the study period are detailed in Appendix 6 for Calvert Hills sites and Appendix 7 for Townsville sites. Rainfall during the previous 1 day, 1-3 days, 3-7 days, 7-30 days, 30-60 days, 60-90 days to the sample and during the following 30 days from the sample were calculated from rainfall records at Calvert Hills Homestead (except for May 1989 to December 1990 when records were obtained from neighbouring Wollogorang station approximately 50km east of Calvert Hills Station; see Figure 2.1), and from Townsville airport records. Rainfall and climatic data for Calvert Hills and Townsville have been presented in section 2.3, while rainfall variables

used for these analyses are presented in Appendix 8 for Calvert Hills sites and Appendix 9 for Townsville sites.

Relationships between the number of toads of each age category active on a sampling night and the recorded environmental variables were determined using a maximum r^2 multiple regression using the statistical package SAS 6.04 (SAS Institute 1995).

5.2.4 Seasonal Changes in Toad Size.

Toads sampled during the mark-recapture study (Chapter 4) had their snout-vent length (SVL) measure to the nearest millimetre on a wooden measuring board (see section 4.2 for collection procedure). Two sites were used at Calvert Hills (Big Calvert River and Homestead) and three at Townsville (Bentley Lagoon, Rock Road Dam and Bell's Dam) (sections 2.1.1 and 2.2.2). Seasonal criteria was determined from previous 30 day and following 30 day rainfall records (section 2.3.1).

To determine if site, season or sex affected mean size of adult toads, a three-way analysis of variance with replication was performed on SVL for toads from Calvert Hills and Townsville separately. In addition, to determine if site or season affected size of sub-adult and/or juvenile toads a two-way analysis of variance with replication was performed on sub-adult and juvenile toads from both locations separately. Sex was not incorporated into the sub-adult or juvenile analyses because it could not be accurately determined (see Chapter 4, section 4.2.2)

Due to unbalanced data sets, only type III sums of squares were used in the analysis. All statistical analysis was performed using SAS 6.04 (SAS Institute 1995).

5.3 Results.

5.3.1 Seasonal Toad Activity.

The proportion of active toads in each age category varied considerably between seasons (Table 5.1). However, more toads were active alongside water courses (within a 1000m^2 transect) in each age category sampled during the study in the late-wet/early-dry season at Calvert Hills (77.4%) and in the late-dry season at Townsville (33.7%) The lowest activity recorded was during the middle-dry season (Calvert Hills 2.7%; Townsville 8.4%).

Table 5.1. Average number and percentage of male, female, sub-adult, juvenile toads, and all age categories combined, active within a 1000m^2 transect at Calvert Hills and Townsville for the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons.

Season	Age		Males		Females		Sub-adults		Juveniles	
	No.	%	No.	%	No.	%	No.	%	No.	%
Calvert Hills										
Early-wet	429	9.2	47	10.9	24	5.6	207	48.3	151	35.2
Middle-wet	190	4.1	89	46.8	26	13.7	8	4.2	67	35.3
Late-wet/Early-dry	3618	77.4	539	14.9	293	8.1	1562	43.2	1224	33.8
Middle-dry	124	2.7	16	12.9	3	2.4	60	48.4	45	36.4
Late-dry	315	6.7	91	28.9	67	21.3	121	38.4	36	11.4
Townsville										
Early-wet	1572	15.9	819	52.1	337	21.4	407	25.9	9	0.6
Middle-wet	1801	18.2	1171	65	108	6	280	15.6	242	13.4
Late-wet/Early-dry	2361	23.8	1374	58.3	159	6.7	477	20.2	351	14.9
Middle-dry	830	8.4	492	59.3	135	16.3	127	15.3	76	9.1
Late-dry	3336	33.7	1290	38.7	358	10.7	1341	40.2	247	10.4

Percentage frequency histograms of adult, sub-adult and juvenile toads active within a 1000m^2 transect during each season clearly demonstrate differences in toad population structure between Calvert Hills and Townsville (Figure 5.1).

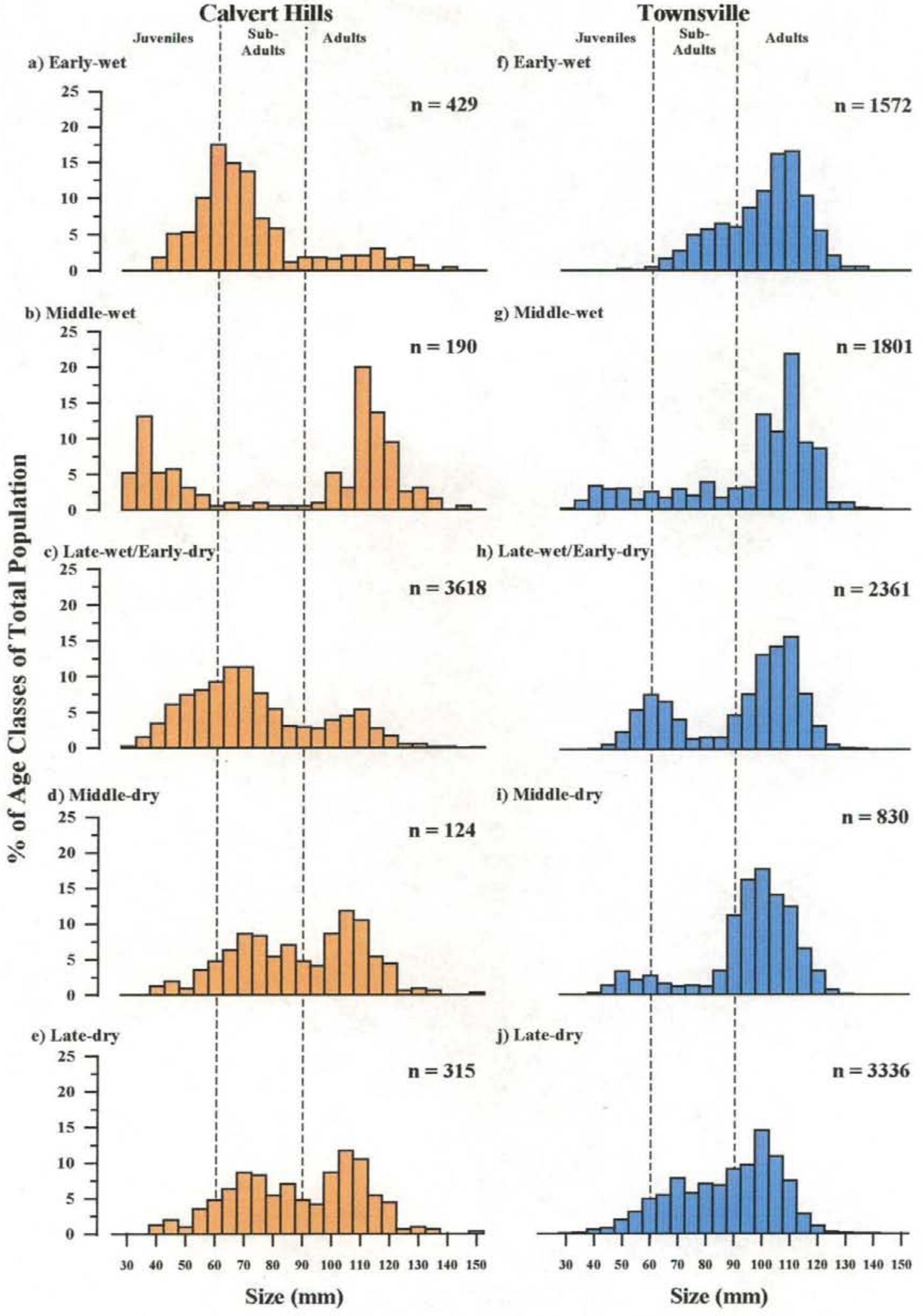
During the middle-wet season at Calvert Hills the population structure split into clear juvenile and adult peaks. These peaks converge over the next three seasons (late-wet/early-dry, middle-dry and late-dry seasons), culminating in a high proportion of sub-adult and juvenile toads in the early-wet. The number of adult toads active within a 1000m^2 transect was highest during the middle-wet.

In Townsville, higher proportions of adult toads were active within a 1000m^2 transect throughout all seasons in comparison to Calvert Hills. The percentage and size of juvenile toads fluctuated during each season with very low proportions active within a 1000m^2 transect in the early-wet season. Fluctuations in juvenile toad activity peaks represent corresponding changes in sub-adult toad proportions. A bimodal distribution of non-adult and adults occurred during the late-wet/early-dry with a similar but less obvious occurrence in the middle dry season.

Figure 5.1. Size frequency distribution of the percentage of age classes of toad population sampled during each season at Calvert Hills (red) and Townsville (blue).

a) Calvert Hills: Early-wet Season;
b) Calvert Hills: Middle-wet Season;
c) Calvert Hills: Late-wet/Early-dry Season;
d) Calvert Hills: Middle-dry Season;
e) Calvert Hills: Late-dry Season;
f) Townsville: Early-wet Season;
g) Townsville: Middle-wet Season;
h) Townsville: Late-wet/Early-dry Season;
i) Townsville: Middle-dry Season;
j) Townsville: Late-dry Season.

Dashed lines mark the size intervals between juvenile, sub-adult and adult toads.


Calvert Hills
Juveniles
Sub-Adults
Adults
a) Early-wet
n = 429
b) Middle-wet
n = 190
c) Late-wet/Early-dry
n = 3618
d) Middle-dry
n = 124
e) Late-dry
n = 315
Townsville
Juveniles
Sub-Adults
Adults
f) Early-wet
n = 1572
g) Middle-wet
n = 1801
h) Late-wet/Early-dry
n = 2361
i) Middle-dry
n = 830
j) Late-dry
n = 3336
% of Age Classes of Total Population
0
5
10
15
20
25
30
40
50
60
70
80
90
100
110
120
130
140
150
Size (mm)
Size (mm)

The number of toads active within a 1000m^2 transect on a given sampling night was found to be significantly affected by location, age category and season, as well as all interactions of the main effects (Table 5.2).

Table 5.2. Summary of three-way ANOVA on the number of toads active within a 1000m^2 transect at Calvert Hills and Townsville with sites pooled. (* = significant at 0.05 level).

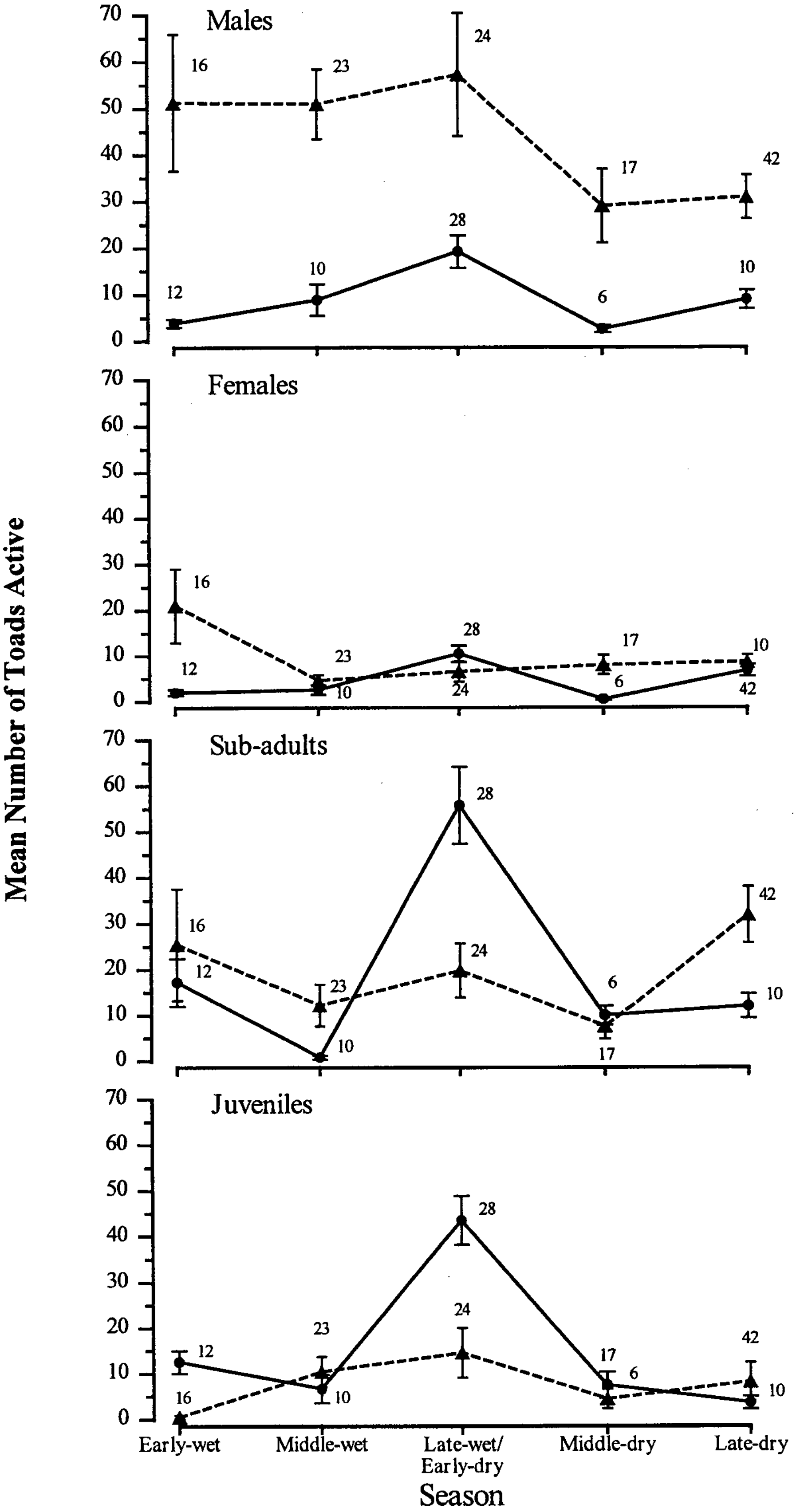
	Calvert Hills x Townsville			
	d.f.	**MS**	**F**	***P***
Location	1	9844.93	15.11	0.0002*
Season	4	8664.31	12.08	0.0001*
Age Category	3	101185.87	14.18	0.0001*
Location* Season	4	3893.58	5.86	0.0003*
Location*Age Category	3	12020.76	16.85	0.0001*
Season*Age Category	12	1379.31	1.95	0.0298*
Location*Season*Age Category	12	1534.24	2.12	0.0135*
Error (Residual)	712	720.47	-	-

The number of toads active within a 1000m^2 transect was highest during the late-wet/early-dry ($\bar{x}$ = 28.72, SE = 2.63, n = 208) and lowest during the middle-dry season ($\bar{x}$ = 10.43, SE = 1.89, n = 92). During the other seasons the highest number of toads active within a 1000m^2 transect occurred in the early-wet ($\bar{x}$ = 17.87, SE = 3.32, n = 112), followed by the late-dry ($\bar{x}$ = 17.62, SE = 1.82, n = 208), and the middle-wet season ($\bar{x}$ = 15.08, SE = 2.21, n =132).

Regardless of location, males were usually more active within a 1000m^2 transect on any given night than any other age category ($\bar{x}$ = 31.61, SE = 2.31, n = 188). The number of sub-adult toads active within a 1000m^2 transect was second ($\bar{x}$ = 24.41, SE = 1.78, n = 188), juvenile toads third ($\bar{x}$ = 13.53, SE = 0.99, n = 188), while females demonstrated the lowest overall activity on any given sampling night ($\bar{x}$ = 8.06, SE = 0.59, n = 188). The number of toads active within a 1000m^2 transect at Townsville was significantly greater than at Calvert Hills (Townsville: $\bar{x}$ = 20.33, SE = 1.51, n = 488; Calvert Hills: $\bar{x}$ = 17.69, SE = 1.60, n = 264).

There was a significant interaction between season, age category and location on toad activity (Table 5.2). The number of male and female toads active within a 1000m^2 transect remained relatively stable from the early-wet through to the late-dry season (Figure 5.2). However, at Calvert Hills, the number of sub-adult and juvenile toads active showed a dramatic increase in the late-wet/early-dry season. This result contrasted activity patterns of sub-adult and juvenile toads at Townsville.

Figure 5.2. Mean number of male, female, sub-adult and juvenile toads active within a $1000m^2$ transect during the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons at Calvert Hills (●, solid line) and Townsville (▲, dashed line). (Standard errors and sample sizes are included).


Males
Females
Sub-adults
Juveniles
Mean Number of Toads Active
0
10
20
30
40
50
60
70
Early-wet
Middle-wet
Late-wet/ Early-dry
Middle-dry
Late-dry
Season
16
23
24
17
42
12
10
28
6
10

5.3.2 Age Categories and Sex Ratios.

At Calvert Hills, season significantly affected the ratio of male to female active within a 1000m^2 transect ($\chi^2 = 14.70$, 4 df, $P = 0.0054$). The number of males active within a 1000m^2 transect outnumbered females in all seasons (Figure 5.3a). The proportion of active adult toads (males and females), to active non-adult toads (sub-adults and juveniles) varied significantly between seasons ($\chi^2 = 259.93$, 4 df, $P = <0.0001$). Adult toad activity was only higher than non-adult toad activity during the middle-wet and late-dry seasons (Figure 5.3b).

Over the five seasons at Townsville, a significantly higher proportion of males were active within a 1000m^2 transect compared to females ($\chi^2 = 261.87$, 4 df, $P = <0.0001$) (Figure 5.3a). The proportion of adult toads to non-adult toads active within a 1000m^2 transect also varied significantly between seasons ($\chi^2 = 449.28$, 4 df, $P = <0.0001$), but, in contrast to Calvert Hills, adult toad activity was higher than non-adult toads during all seasons except the late-dry season (Figure 5.3b).

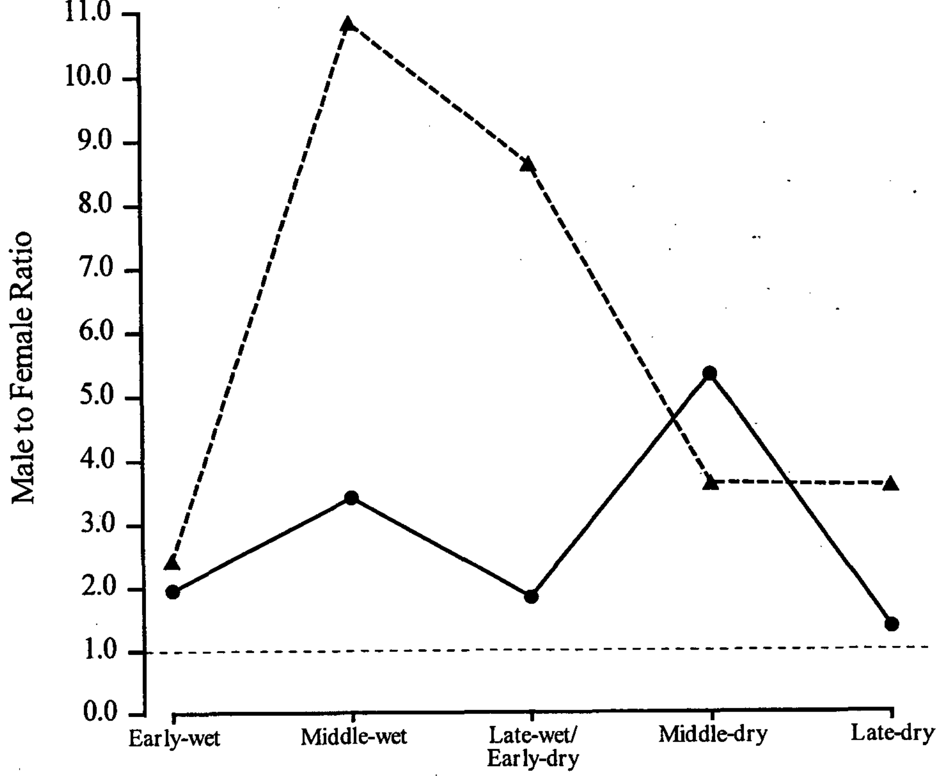
Figure 5.3a. Proportion of male to female toads active within a 1000m^2 transect during early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons during study. (The short dashed horizontal line indicates the point where the male to female ratio is equal).

Calvert Hills = ●, solid line;
Townsville = ▲, dashed line.

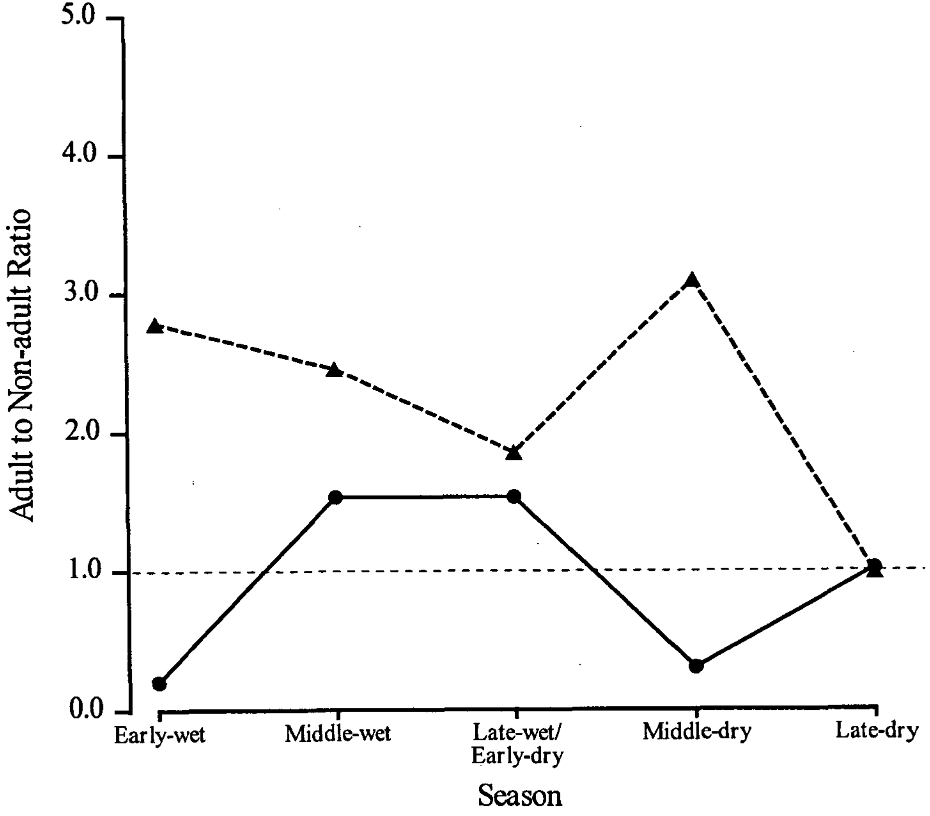
Figure 5.3b. Proportion of adult to non-adult toads within a 1000m^2 transect during early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons during study. (The short dashed horizontal line indicates the point where the adult to non-adult ratio is equal).

Calvert Hills = ●, solid line;
Townsville = ▲, dashed line.

a) Male to Female Ratio



b) Adult to Non-adult Ratio



5.3.3 Environmental Factors Affecting Toad Activity.

Relationships among environmental variables and toad densities are summarised in Table 5.3. The majority of significant variables on toad activity of all age categories at both locations were rainfall related. However, only a negative correlation of rainfall the previous 3-7 and 7-30 days for female and sub-adults, and a positive correlation of rainfall in the previous 60-90 days for sub-adults were the same for each location. All other significant correlations were unique to that locality. No obvious pattern was observed for non-rainfall related variables. (Results of analyses are detailed in Appendix 10 for Calvert Hills and Appendix 11 for Townsville).

In summary, toad activity for all age categories decreased at Calvert Hills as recent rainfall (previous 3-30 days) increased. For all age categories except juveniles, toad activity increased as rainfall in the previous 30-60 days increased. The number of sub-adult and juvenile toads active also increased as rainfall in the previous 60-90 days increased. Furthermore, with an increase in rainfall in the following 30 days, the activity of all toads except juveniles increased.

Except for males, toad activity decreased at Townsville as recent rainfall (previous 3-30 days) increased. The activity of female and sub-adult toads increased as previous 60-90 day rainfall increased. However, the number of females active decreased as previous 30-60 day rainfall and following 30 day rainfall increased. Male activity was not correlated with any of the environmental variables measured.

Table 5.3. Correlations (found via a maximum r^2 regression) of environmental variables with the number of toads active at Calvert Hills and Townsville. (+ = positive correlation; − = negative correlation; blank squares indicate no significant correlation; diagonal lines indicate the same results for Calvert Hills and Townsville).

Variables	Calvert Hills				Townsville			
	Males	Females	Sub-adults	Juveniles	Males	Females	Sub-adults	Juveniles
Air Temperature			−					
Soil Temperature at 10m			+					
% Cloud Cover	−							−
Humidity %	+							
Rainfall Previous 1 Day								
Rainfall Previous 1-3 Days								
Rainfall Previous 3-7 Days	−	▨ −	▨ −			▨ −	▨ −	−
Rainfall Previous 7-30 Days	−	▨ −	▨ −	−		▨ −	▨ −	
Rainfall Previous 30-60 Days	+	+	+			−		
Rainfall Previous 60-90 Days			▨ +	+		+	▨ +	
Rainfall Following 30 Days	+	+	+			−		
Maximum r^2 (%) of Toad Density	56.5	64.4	60.9	41.9	-	20.4	29	11

5.3.4 Seasonal Changes in Body Size.

5.3.4.1 Adult Toads.

At Calvert Hills all effects of site, season and sex were significant on the size of adult toads except site as a main effect, site by sex interaction and the site by season by sex interaction (Table 5.4). At Townsville all effects of site, season and sex were significant except the site by sex interaction (Table 5.4).

No significant site effect was observed for Calvert Hills (Table 5.4). However, a significant effect on adult mean SVL was recorded at Townsville sites with toads at Bell's Dam ($\bar{x}$ = 106.83, SE = 0.23, n = 1423) being larger than those at Rock Road Dam ($\bar{x}$ = 104.21, SE = 0.16, n = 2595). Mean adult length of toads was smallest at Bentley Lagoon ($\bar{x}$ = 101.47, SE = 0.15, n = 2341).

Table 5.4. Three-way ANOVA results for mean adult toad size against site, season and sex (males & females). (* = significant at 0.05 level).

	Calvert Hills				Townsville			
	d.f.	MS	F	*P*	d.f.	MS	F	*P*
Site	1	163.79	1.76	0.1846	2	5241.2	99.98	0.0001*
Season	4	1238.1	13.32	0.0001*	4	2489	47.48	0.0001*
Sex	1	2338.5	25.17	0.0001*	1	1853.6	35.36	0.0001*
Site*Season	4	482.13	5.19	0.0004*	8	1323.9	25.25	0.0001*
Site*Sex	1	29.92	0.32	0.5705	2	98.84	1.89	0.1518
Season*Sex	4	284.63	3.06	0.0159*	4	180.91	3.45	0.0080*
Site*Season*Sex	4	87.18	0.94	0.4409	8	139.82	2.67	0.0064*
Error (Residual)	1140	92.92	-	-	6329	52.42	-	-

There was a significant seasonal effect on mean adult toad SVL at both Calvert Hills and Townsville. Mean adult size at Calvert Hills reached a maximum during the middle-wet season. There was little variation in size during the late-wet/early-dry, middle-dry and late-dry seasons (range 104.95 to 105.85mm), but an increase occurred in the early-wet.

The mean SVL of adult toads at Townsville was also highest in the middle-wet and lowest during the middle- and late-dry seasons. Size in the early and late-wet/early-dry were similar (range 103.93 to 104.88), as was size in the middle- and late-dry season (range 101.06 to 101.47). Mean toad size at Calvert Hills was always greater than at Townsville. Toad SVL followed a similar trend at both locations with larger mean toad length recorded in the two wet season samples (ie. early- and middle-wet season).

The mean size of males was always smaller than females at both Calvert Hills (males: $\bar{x}$ = 105.51, SE = 0.29, n = 748; females: $\bar{x}$ = 108.49, SE = 0.64, n = 412) and Townsville (males: $\bar{x}$ = 103.58, SE = 0.10, n = 5275; females: $\bar{x}$ = 104.80, SE = 0.31, n = 1084).

There was a significant interaction between site and season at both localities on mean body size (Table 5.4). Mean toad size was usually greater at Homestead than at Big Calvert River (Figure 5.4a). There were two notable exceptions. In the early-wet and middle-dry mean toad size was smaller at Homestead.

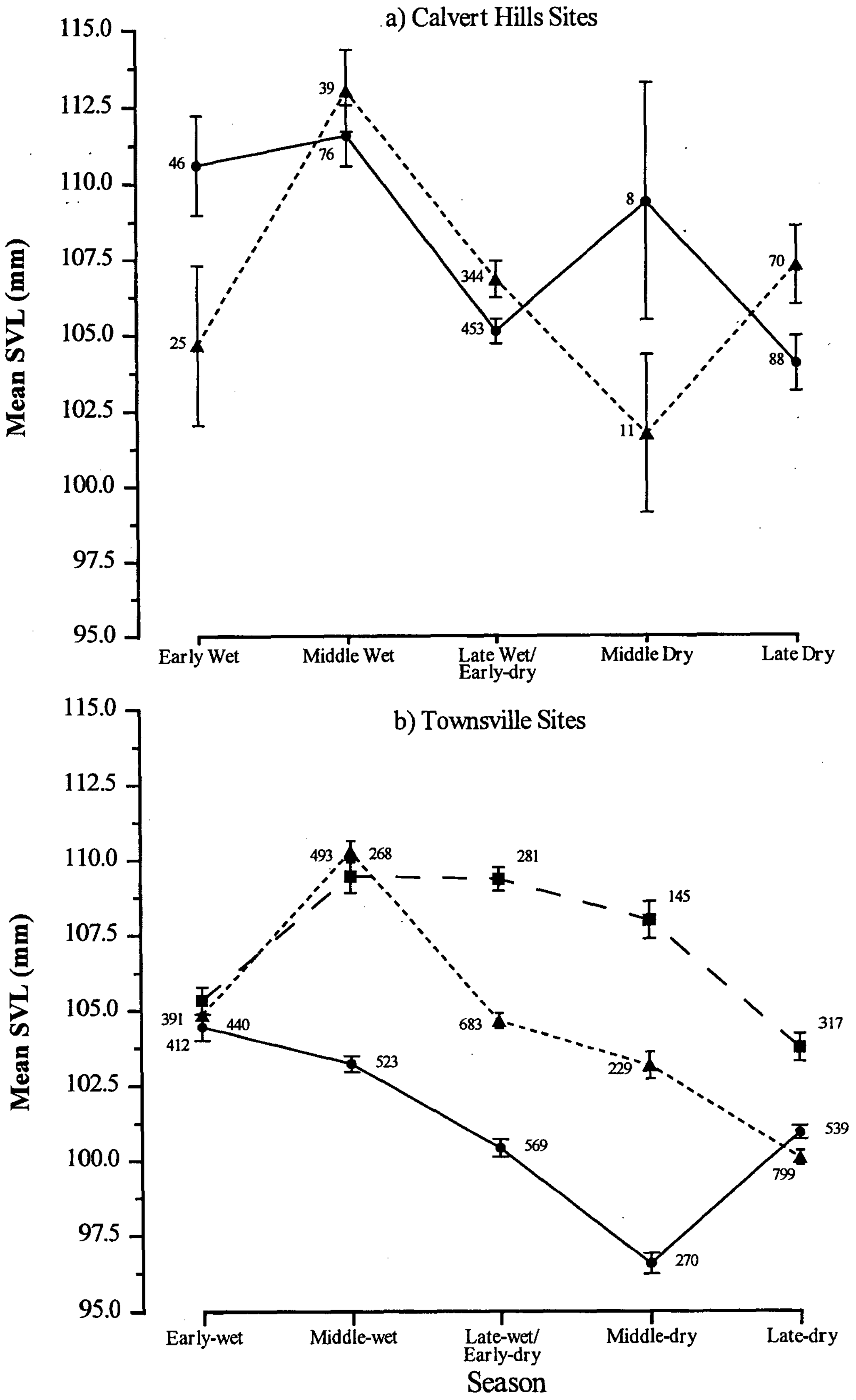
At Townsville, two sites showed similar trends in mean size over seasons (Figure 5.4b). At Bell's Dam and Rock Road Dam mean size increased the from early-wet to middle-wet then decreased for the rest of the seasons. However, at Bentley Lagoon populations decreased in mean size from early-wet to middle-dry but increased sharply from middle-dry to the late-dry season.

Figure 5.4a. Mean adult SVL at Calvert Hills sites during the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons. (Standard errors and sample sizes are included).

Big Calvert River = ●, solid line;
Homestead = ▲, dashed line).

Figure 5.4b. Mean adult SVL at Townsville sites during the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons. (Standard errors and sample sizes are included).

Bentley Lagoon = ●, solid line;
Rock Road Dam = ▲, short dashed line;
Bell's Dam = ■, long dashed line.


a) Calvert Hills Sites
Mean SVL (mm)
115.0
112.5
110.0
107.5
105.0
102.5
100.0
97.5
95.0
46
25
39
76
344
453
8
11
70
88
Early Wet
Middle Wet
Late Wet/
Early-dry
Middle Dry
Late Dry
b) Townsville Sites
Mean SVL (mm)
115.0
112.5
110.0
107.5
105.0
102.5
100.0
97.5
95.0
391
412
440
493
268
523
281
683
569
145
229
270
317
539
799
Early-wet
Middle-wet
Late-wet/
Early-dry
Middle-dry
Late-dry
Season

There was a significant interaction between season and sex at both Calvert Hills and Townsville (Table 5.4). These interactions for male and female toads are illustrated in Figure 5.5a (Calvert Hills) and 5.5b (Townsville).

At Calvert Hills there was also a general trend of decreasing of mean body size from the early-wet to the late-dry. However, mean female body size show a significantly different trend with sharp rises in mean body length during the middle-wet and an even more pronounced increase during the middle dry. However, this latter increase is probably a reflection of small sample size (n = 3) as trends on small numbers are not representative of interactions (after Roth and Ráb 1987).

At Townsville, both males and females follow similar trends apart from the middle-dry when female mean body length does not decrease as much as male body length. The significance of this interaction is difficult to determine but probably occurs during the middle-dry season where mean female size does not show a marked decline compared to male size.

The interaction of season, site and sex was only significant at Townsville (Table 5.4) and is illustrated in Figure 5.6.

Mean body size of males at all three sites follow similar trends as the site by season interaction shown in Figure 5.4b with a similar trend shown for Bell's Dam and Rock Road Dam (ie. mean size increasing from early-wet to middle-wet and then decreasing during the next three seasons), and a different trend shown at Bentley Lagoon (ie. decrease in mean size from early-wet to the middle-dry followed by an increase into the late-dry). This interaction suggests that males are responsible for the effects shown in Figure 5.4b.

Figure 5.5 Male and female mean SVL of males (●, solid line) and females (▲, dashed line) during the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons. (Standard errors and sample sizes are included).

a) Calvert Hills;
b) Townsville.

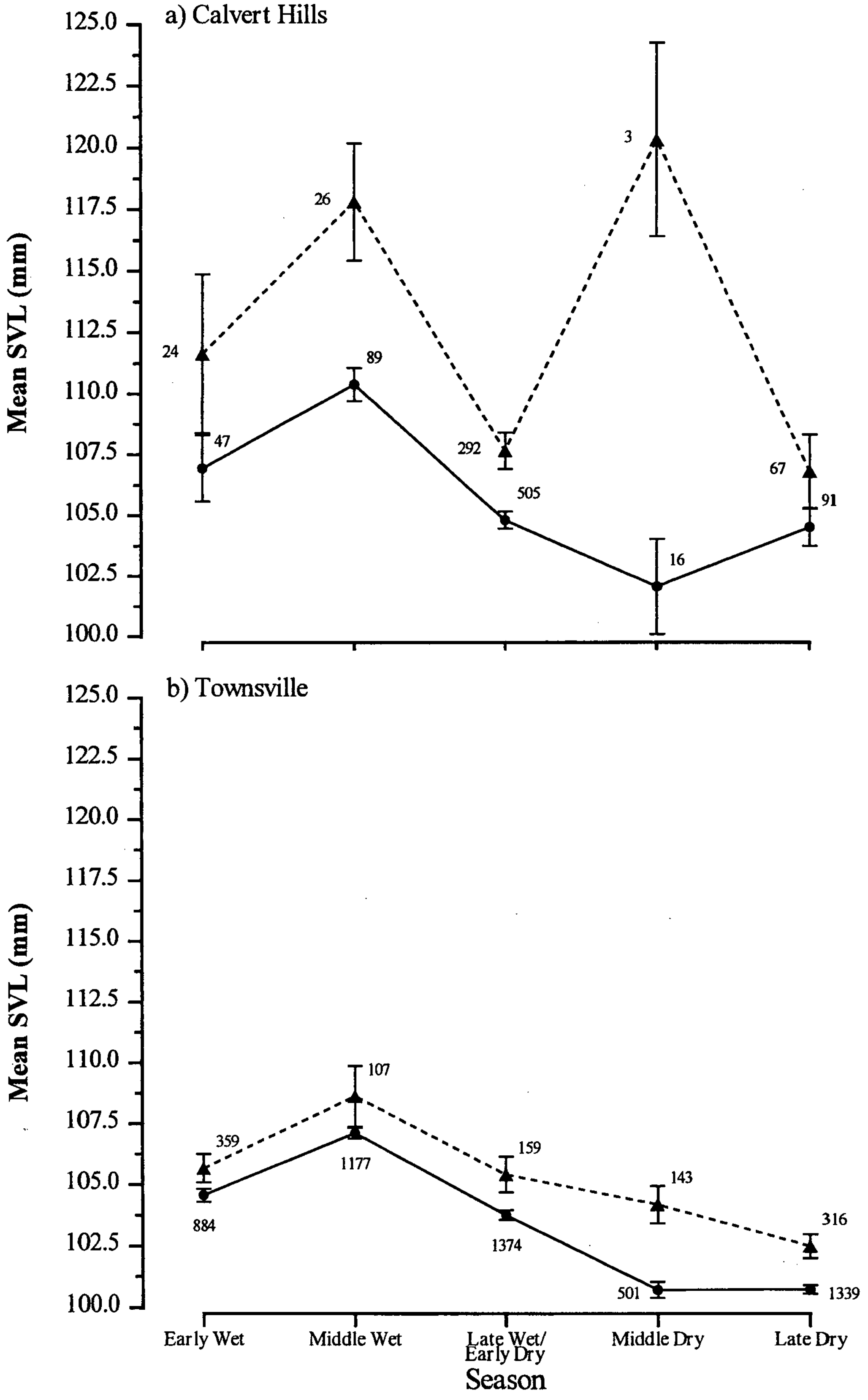
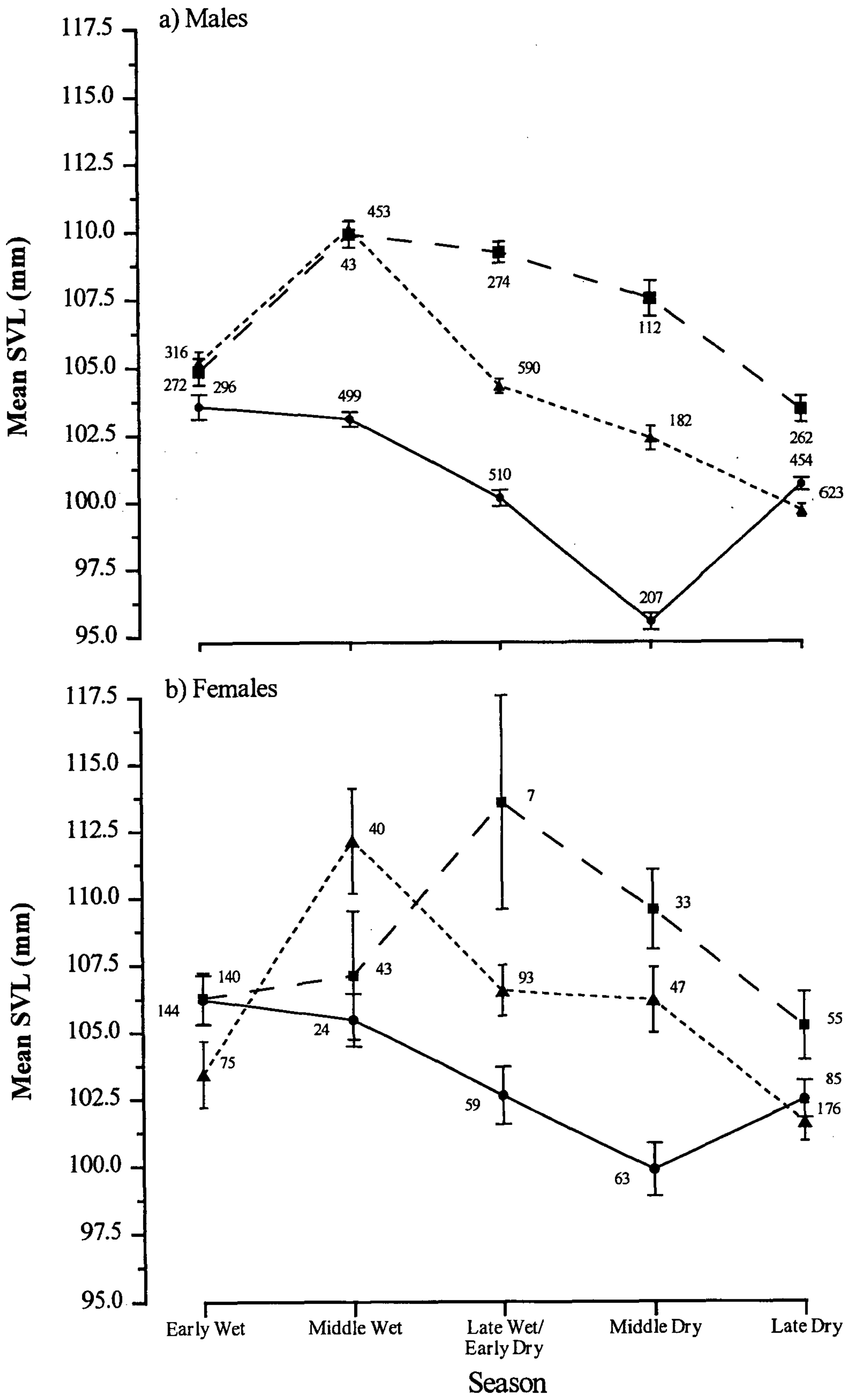

a) Calvert Hills
Mean SVL (mm)
125.0
122.5
120.0
117.5
115.0
112.5
110.0
107.5
105.0
102.5
100.0
24
26
3
292
67
47
89
505
16
91
b) Townsville
Mean SVL (mm)
125.0
122.5
120.0
117.5
115.0
112.5
110.0
107.5
105.0
102.5
100.0
359
107
159
143
316
884
1177
1374
501
1339
Early Wet
Middle Wet
Late Wet/
Early Dry
Middle Dry
Late Dry
Season

Figure 5.6. The mean SVL of adult toads at Townsville sites during the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season. (Standard errors and sample sizes are included).

Bentley Lagoon = ●, solid line;
Rock Road Dam = ▲, short dashed line;
Bell's Dam = ■, long dashed line.

a) Males;
b) Females.


a) Males
Mean SVL (mm)
117.5
115.0
112.5
110.0
107.5
105.0
102.5
100.0
97.5
95.0
453
43
274
112
316
272
296
590
499
182
262
454
510
623
207
b) Females
Mean SVL (mm)
117.5
115.0
112.5
110.0
107.5
105.0
102.5
100.0
97.5
95.0
7
40
33
140
43
93
47
144
24
55
75
85
176
59
63
Early Wet
Middle Wet
Late Wet/ Early Dry
Middle Dry
Late Dry
Season

Mean female body size at Rock Road Dam and Bentley Lagoon closely follow the trends shown by males at the same sites. Bell's Dam however, does not follow the same trend with female body length increasing during the late-wet/early-dry instead of the middle-wet season and then decreasing through to the late-dry.

5.3.4.2 Sub-adult Toads.

The results from the two-way ANOVA of site and season on sub-adult SVL from Calvert Hills and Townsville are summarised in Table 5.5. All effects and interactions of site and season from this ANOVA were significant except the effect of site at Calvert Hills.

Table 5.5. Two-way ANOVA results for sub-adult toad size against site and season at Calvert Hills and Townsville. (* = significant at 0.05 level).

	Calvert Hills				Townsville			
	d.f.	MS	F	*P*	d.f.	MS	F	*P*
Site	1	86.95	1.53	0.2166	2	964.74	14.13	0.0001*
Season	4	1067.4	18.76	0.0001*	4	3037.9	44.49	0.0001*
Site*Season	4	178.88	3.14	0.0138*	8	14.13	20.56	0.0001*
Error (Residual)	1949	56.9	-	-	2867	68.29	-	-

Sub-adult toads at Bentley Lagoon ($\bar{x}$ = 74.04, SE = 0.27, n = 1145) were slightly smaller than those at Rock Road Dam ($\bar{x}$ = 75.38, SE = 0.27, n = 1066) and Bell's Dam ($\bar{x}$ = 75.34, SE = 0.32, n = 671). The difference in sub-adult toad size between sites is probably not biologically significant but caused by the effects of measurement errors.

At Calvert Hills mean sub-adult size increased from the early-wet to the middle-wet and from the late-wet/early-dry, but decreased from the middle-wet to late-wet/early dry and from the middle-dry to the late-dry. There was, however, a general trend for increasing size from the early-wet through to the late-dry.

At Townsville sub-adult SVL was largest in the middle-dry and smallest in the late-wet/early-dry season. Sub-adult size decreased from the early-wet to the late-wet/early-dry season, increased in the middle-dry and then decreased again into the late-dry season.

The mean SVL of sub-adult toads at Calvert Hills sites are illustrated in Figure 5.7a. Mean sub-adult body size at both sites shows a general increasing trend from the early-wet through to the late-dry season. There are two exceptions to this trend. A sharp increase in mean sub-adult size occurs at Big Calvert River during the middle-wet, which is probably a reflection of small sample size (n = 2), and a decrease in mean size at Homestead in the late-dry season.

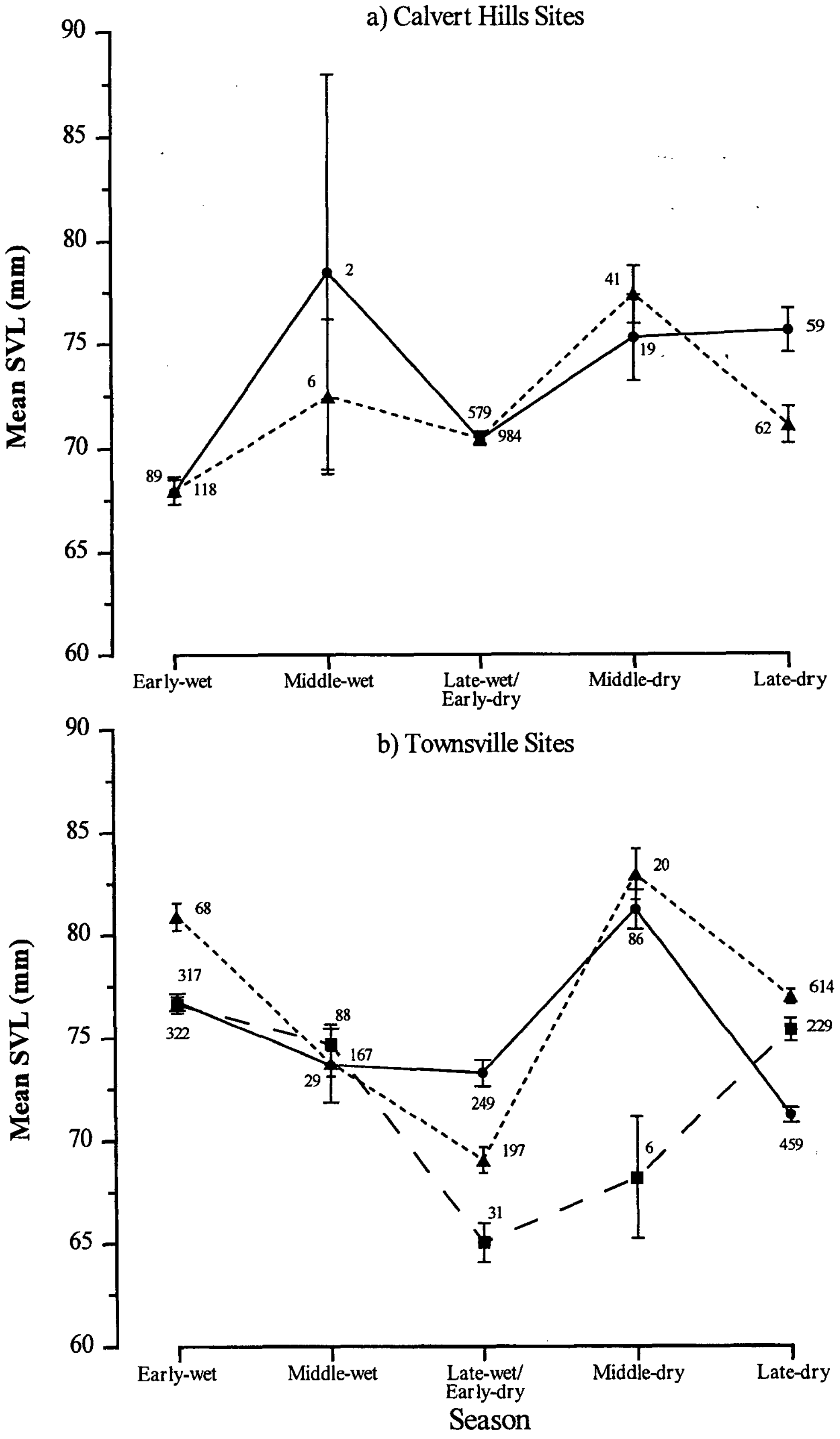
The mean SVL of sub-adult toads at Townsville sites is illustrated in Figure 5.7b. Mean sub-adult body size at Bentley Lagoon and Rock Road Dam follow similar trends, decreasing from the early-wet to the late-wet/early-dry, rising sharply in the middle-dry, and then decreasing again into the late-dry season. Mean body size at Bell's Dam also decreases from the early-wet to the late-wet/early-dry but does not show a sharp rise in the middle-dry but instead shows a gradual increase into the middle-dry and again into the late-dry season. In the late-dry season mean sub-adult body size is similar at all sites.

Figure 5.7a. Mean sub-adult SVL at Calvert Hills sites in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season. (Standard errors and sample sizes are included).

Big Calvert River = ●, solid line;
Homestead = ▲, dashed line.

Figure 5.7b. Mean sub-adult SVL at Townsville sites in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season. (Standard errors and sample sizes are included).

Bentley Lagoon = ●, solid line;
Rock Road Dam = ▲, short dashed line;
Bell's Dam = ■, long dashed line.


a) Calvert Hills Sites
Mean SVL (mm)
90
85
80
75
70
65
60
2
6
41
59
19
579
984
62
89
118
Early-wet
Middle-wet
Late-wet/
Early-dry
Middle-dry
Late-dry
b) Townsville Sites
Mean SVL (mm)
90
85
80
75
70
65
60
20
68
86
317
614
88
229
322
167
29
249
197
6
459
31
Early-wet
Middle-wet
Late-wet/
Early-dry
Middle-dry
Late-dry
Season

5.3.5.3 Juvenile Toads.

The results from the two-way ANOVA of site and season on juvenile SVL from Calvert Hills and Townsville are summarised in Table 5.6. All effects and interactions of site and season from the two-way ANOVA performed on juvenile toads were significant except the effect of site at Calvert Hills.

Table 5.6. Two-way ANOVA results for juvenile toad size against site and season at Calvert Hills and Townsville. (* = significant at 0.05 level).

	Calvert Hills				Townsville			
	d.f.	MS	F	*P*	d.f.	MS	F	*P*
Site	1	0.33	0	0.9565	2	155.48	4.84	0.0081*
Season	4	2863.8	25.95	0.0001*	4	2746.7	85.46	0.0001*
Site*Season	4	275.7	2.5	0.0410*	8	158.28	4.92	0.0001*
Error (Residual)	1547	110.35	-	-	1035	32.14	-	-

Juvenile SVL was lowest at Bell's Dam ($\bar{x}$ = 48.57, SE = 0.55, n = 216). Rock Road Dam sub-adults were larger ($\bar{x}$ = 50.66, SE = 0.34, n = 410), while Bentley Lagoon sub-adult toads were the largest ($\bar{x}$ = 51.41, SE = 0.29, n = 424).

Similar trends in mean juvenile SVL occurred at both locations with the largest size recorded in the early-wet and lowest in the middle-wet season. Size increased from the middle-wet through to the following early-wet season. Juvenile toads were larger at Townsville that at Calvert Hills in all five seasons.

Mean juvenile SVL showed similar trends in the early, middle and late-wet/early-dry seasons at both Calvert Hills sites (Figure 5.8a). However, mean SVL decreased after the late-wet/early-dry at Big Calvert River but did not change during the same period at Homestead. Again this is probably a reflection of small sample size (n = 5) and may not be biologically significant.

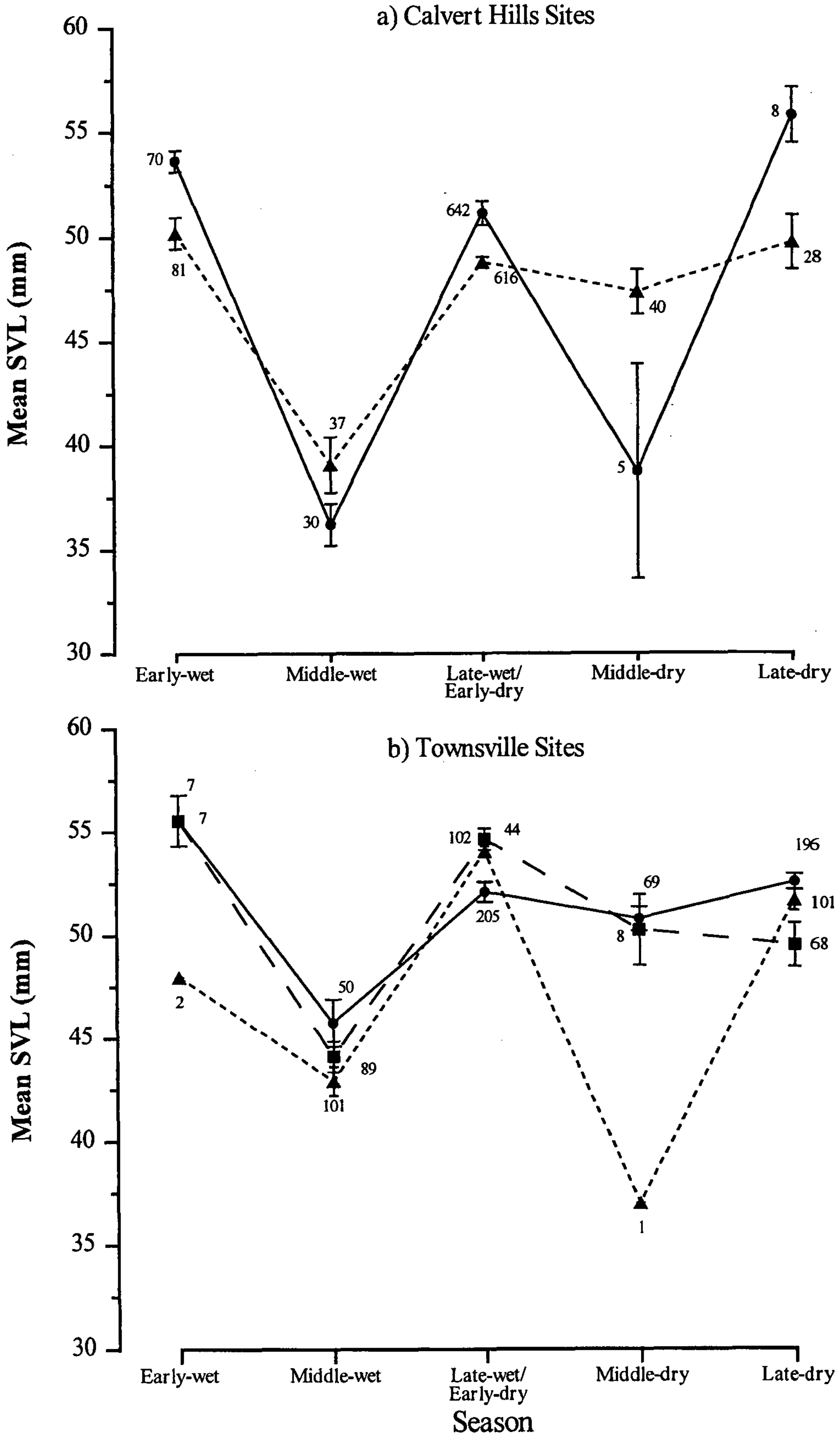
Townsville sites followed similar trends during the five seasons at all sites except for the one juvenile sample at Rock Road Dam in the middle-dry season when a larger decrease was recorded (Figure 5.8b). This result is also probably a reflection of small sample size (n = 1) and may not be biologically significant.

Figure 5.8a. The mean SVL of juvenile toads at Calvert Hills sites in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons. (Standard errors and sample sizes are included).

Big Calvert River = ●, solid line;
Homestead = ▲, dashed line.

Figure 5.8b. The mean SVL of juvenile toads at Townsville sites in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons. (Standard errors and sample sizes are included).

Bentley Lagoon = ●, solid line;
Rock Road Dam = ▲, short dashed line;
Bell's Dam = ■, long dashed line.


a) Calvert Hills Sites
Mean SVL (mm)
60
55
50
45
40
35
30
70
81
37
30
642
616
40
5
8
28
Early-wet
Middle-wet
Late-wet/
Early-dry
Middle-dry
Late-dry
b) Townsville Sites
Mean SVL (mm)
60
55
50
45
40
35
30
7
7
2
50
89
101
102
44
205
69
8
1
196
101
68
Early-wet
Middle-wet
Late-wet/
Early-dry
Middle-dry
Late-dry
Season

5.4 Discussion.

5.4.1 Seasonal Variation in Toad Activity.

Although there was considerable variation between sites, seasons and locations, the number of *B. marinus* per 1000m^2 active along water sources was generally higher at Townsville than at Calvert Hills. In addition, males made up the majority of toads active around Townsville sites, whereas sub-adults made up the majority at Calvert Hills.

The most likely explanation for regional variation in the number of adult and non-adult toads active within the sampling area is the differences in climate between Calvert Hills and Townsville. The wet season at Calvert Hills is usually shorter than in Townsville (Figure 2.4), and therefore may result in a shorter breeding season for toads. As the majority of breeding occurs during the wet season (Zug and Zug 1979; Hearnden 1991), high numbers of smaller-sized cohorts may enter the sampling area and survive through to the end of the wet season and into the dry season. However, high numbers of non-adult toads active at Calvert Hills were not sustained throughout the dry season. This suggests that climatic factors, such as high diurnal temperatures and prolonged dry periods that are characteristic of Calvert Hills, probably severely decrease the activity of these cohorts thus making survival through to the following wet season difficult. Mortality of smaller toads at this time is expected to be high because of their higher surface area/volume ratios and subsequent effects of hydric stress being higher for smaller toads than larger toads during these dry periods.

In contrast to Calvert Hills, the number of males active was higher while the number of non-adults active was lower at Townsville sites. Fluctuations in activity, due to environmental extremes as outlined above, may not be as severe at Townsville. Furthermore, with a longer period of rain during the wet season at Townsville, the potential

breeding season of toads may therefore be longer. In addition, with a longer breeding season, the influx of smaller-sized toads may not have been concentrated during a single period but spread over several months in the wet season and early in the dry season.

The high number of toads active in the late-wet/early-dry season at Calvert Hills (Figure 5.1) was primarily due to large numbers of sub-adult and juvenile toads active within the sampling area. The ratio of non-adult to adult toads active along water courses was especially skewed early in the wet season (Figure 5.3b). Metamorphs, that have emerged from their natal pools during the wet season, show rapid growth (see Chapter 3), and are therefore increasing the number of smaller cohorts active along water courses. Ovaska (1991) reported a similar trend in a tropical frog, *Eleutherodactylus johnstonei*, where juvenile numbers increased in the wet season, reached a peak for a short period, and then declined into the dry season. In addition, stressful environmental extremes experienced at Calvert Hills, especially during the late-wet/early-dry and middle-dry seasons, may have made it necessary for young toads to centre their activity patterns around a water body where they have an opportunity to maintain their hydric requirements.

At Townsville sites the number of male and female toads active was generally higher during wet season samples and lower during dry season samples. This pattern is consistent with most tropical anurans and corresponds to breeding during rainy periods and inactivity and/or mortality during dry periods. However, at Calvert Hills, fewer adults were present at sites in the early-wet than during the middle-wet season. This indicates that the majority of breeding at this location may have already taken place (ie. during the height of the wet season), or the toads are breeding elsewhere. It is unlikely that toads are breeding in other locations as the river habitat is similar along its length and toads do not appear to favor particular areas of river bank to breed. However, as the commencement of the wet season corresponds to higher food abundances (Janzen 1973) adult toads may therefore be spending considerable time foraging away from water sources (Schwarzkopf and Alford

1996). Later in the wet season, after the food abundance has decreased and the toad's energy reserves from feeding activity have increased, male and female toads may be more willing to breed and therefore come down to the water's edge more often.

Regional variation in the number of toads active within a sample may have also been due to site differences. For instance, Townsville populations were sampled around sites (ie. dams) where very little water existed outside these areas. These sites may have acted as home sites for males and these toads may have made regular visits to facilitate breeding and maintain hydric requirements. The estimates of toad activity suggested that large congregations of males were present at an isolated water hole, while other age categories, especially females, may have actively avoided these sites except during periods of extreme hydric stress or when ready to breed. *B. marinus* has previously been shown to have foraging areas, or activity centres, well away from permanent water sources or breeding areas but will return to these water sources during dry periods (Carpenter and Gillingham 1987). In contrast, the two main sites at Calvert Hills (ie. Big Calvert River and Homestead), were situated on semi-permanent rivers and the spacial pattern of populations may have been different causing the observed activity of adult toads per hectare to be considerably lower.

In addition to climatic extremes and hydric requirements, regional and site differences in the number of toads active around water sources may have been caused by the quality and quantity of neighbouring retreat sites. Shortages of retreat sites have previously been shown to limit the number of frogs within a population (Stewart and Pough 1983). Furthermore, *B. marinus* have been shown to select favourable retreat sites according to their hydric qualities (see Chapter 7) and will return to that site on a regular basis. Micro-environmental and physical differences between sites therefore need to be examined in more detail to better explain site variations.

The number of toads active was generally lowest in the middle of the dry season. This may reflect inactivity (ie. toads remaining in refuge sites), and/or mortality. It is not surprising that toads are relatively scarce at this time. The low minimum temperatures in the middle of the dry season, when compared to those experienced during the wet season, lead to depressed activity (Zug and Zug 1979; Schwarzkopf and Alford 1996) with part of the population becoming dormant (Zug *et al.* 1975). For example, nightly temperatures during the middle of the dry season at Calvert Hills averaged approximately 12° C and at Townsville 15-16° C. Furthermore, nightly temperatures were often below these averages thus causing a severe reduction in toad activity. Other toad species, eg. *B. melanostrictus*, also demonstrate reduced activity during the dry and colder seasons in tropical areas (Jørgensen *et al.* 1986).

Although the responses of toads to environmental conditions are flexible and vary among individuals (Preest and Pough 1989), small toads in tropical regions during the middle of the dry season may be forced to be inactive and remain in their shelter sites due to an increased risk of dehydration. Numerous small, dead toads, presumably from dehydration, were often found in shelters or alongside water courses during this season. Mortality from dehydration may account for some decline in the activity of smaller toads, and also possibly larger toads, during the dry compared to the wet season. Juvenile toads for example, select environments that produce body temperatures that tend to minimise their rates of dehydration (Tracey *et al.* 1993). Their numbers will decline as some grow and are recruited into the adult population while others leave the population either by death or emigration (Ovaska 1991). In addition to hydric pressures, during the dry season, food availability is also low during this period (Jansen 1973) which may lead to starvation.

5.4.2 Sex Ratios.

At both Calvert Hills and Townsville sites, there was a significant male-biased sex ratio during all seasons (Figure 5.3a). A male-biased sex ratio of *B. marinus* at water sources, has been previously shown in all seasons (Zug and Zug 1979) or during the wet- and early-dry seasons (Hearnden 1991). The reason for a male-bias sex ratio during this study is possibly due to males arriving earlier and remaining longer at a breeding site, thus creating large male congregations throughout the breeding season, while females will only visit breeding sites when gravid, to breed, and avoid large male congregations at other times. Similarly, male *B. bufo* arrive at breeding ponds earlier and remain throughout the spawning period, while females only stay for a few days (Gittens *et al.* 1980). Other studies on the sex ratio of *B. fowleri* and *B. bufo* suggested that males might reach maturity at an earlier age than females and that females may not breed every year (Christein and Taylor 1978; Breden 1988). Unfortunately this hypothesis could not be applied to *B. marinus* during this study due to the low rates of recapture of female toads (see Chapter 4).

As most breeding occurs during the wet season, often protracted over many months, it is possible that a male toad's presence at a breeding site every night during this period is a selective breeding advantage. Females during the wet season will only visit a breeding to site to breed, ie. on one or possibly two occasions over a few months. Although forgoing opportunities to forage away from water sources during favourable hydric periods during the wet season, an individual male that is constantly present at a breeding site may therefore have a selective advantage by breeding more often. Males may also stay longer at a breeding site to compensate for a high degree of competition for mates as the number of female toads decreases (Salvador and Carrascal 1990). A proportion of males at water sources, even during relatively unfavourable dry conditions, may be a selective advantage to participate in chance breeding outside of the wet season, especially during unseasonal dry season rain.

5.4.3 Effects on Toad Activity.

Rainfall clearly influences toad activity (Table 5.3). The number of toads active from all age categories and from both locations (except males at Townsville), were negatively correlated with rainfall during the previous 3-7 days and/or the previous 7-30 days. That is, toad densities within the sampling areas were lower when there was relatively recent (previous 3-30 days) rainfall. This time probably represents a reduction in hydric stress for toads and most individuals therefore forage away from water sources. The only toads present during this time may have been large adults involved in breeding activity. Carpenter and Gillingham (1987) showed that, during wetter periods, *B. marinus* foraged within an activity centre away from water and obtained all hydric requirements within that area. Their results support the patterns seen during this study.

Except for juvenile toads, the density of all age categories at Calvert Hills were also positively correlated with rainfall during the previous 30-60 days. A positive correlation between toad numbers at a waterhole and time since the last rainfall has been previously shown (Carpenter and Gillingham 1987). According to the seasonal criteria (section 2.3.1), this correlation generally represents the time period between peak wet season rains and the late-wet/early-dry season. It also indicates the time since rain when dehydration stresses will impact on toad populations. After 1-2 months of dry conditions most breeding activity has ceased, and it is essential for toads at Calvert Hills to be near water to rehydrate. A similar correlation did not exist at Townsville and may indicate an extended breeding period compared to Calvert Hills or that the time period for dehydration stress to become apparent at this location is longer than at Calvert Hills. This result provides further support that environmental conditions at Calvert Hills, compared to those experienced at Townsville, had more severe affects on toad activity especially in relation to rehydration.

Male toads at Townsville were not significantly correlated with any of the recorded environmental variables. A possible explanation is that large densities of males will congregate around dams in Townsville regardless of whether it has rained recently or not suggesting that breeding period may be protracted at this location. This result may be due to their high breeding potential at some occasions, hydric stress at others, and some type of site fidelity. Further study, using additional biotic and abiotic factors and their effects on toad populations at Townsville, is required for clarification.

5.4.4 Individual Size Variation.

Mean adult toad size was largest during wet season samples and smallest during dry season samples. As reproduction in *B. marinus* primarily occurs within the wet season (Zug and Zug 1979), this result may indicate that samples during this time contained a higher proportion of large, potentially breeding adults along watercourses. Immediately after the wet season the number of toads active at water sources was highest indicating that smaller adults, that may have avoided breeding congregations in the wet season due to competition and predation risks, and smaller individuals from sub-adult cohorts (Figure 5.1), enter the population around water sources to rehydrate. The influx of smaller sized, younger adults around water sources may therefore explain the decrease in mean body size during dry season samples.

A slight increase in mean SVL of adults occurred at Townsville during the late-dry season. Breeding populations of larger toads at a waterhole in the late-dry would certainly increase adult mean body size at this time. As larger toads are more likely to breed (Hearnden 1991), this result may be due to Townsville toads breeding period commencing earlier and being more protracted, due to more rain over a longer period, than at Calvert Hills. An alternative explanation is that, in Townsville, only the largest toads, and

therefore those in best condition, survive through to the late-dry season. However, the number of toads active at this time suggests that survival through to the end of the dry season is probably more difficult at Calvert Hills because of the more climatic conditions experience. Survival through to the end of the dry season by Townsville toads is probably less stressful thus suggesting both large and small toads survive through the dry to the commencement of the wet season.

Females were significantly larger than males at both Calvert Hills and Townsville. Size dimorphism has been reported on numerous occasions in anurans (eg. Gibbons and McCarthy 1984; Hemelaar 1988; Ritke *et al.* 1991). The adaptive significance of larger female body size is assumed to be related to fecundity because larger females produce larger clutches than smaller females (Gibbons and McCarthy 1986; Halliday and Verrell 1988; Ritke *et al.* 1991). For example, larger females of *B. calamita* produce more numerous, larger eggs (Tejedo 1992b). Greater female size however, might result in differential mortality by increasing stresses associated with egg production and associated rapid loss of condition after oviposition, and by making them more conspicuous to predators (Gittens *et al.* 1980). Thus, there is a trade-off between female size at reproduction and sources of size-related mortality. This trade-off, however, may not be as important for toads in Australia due to the lack of natural predators within their range.

The mean size of sub-adult toads generally increased from the wet season samples through to dry season samples. This result represents an increase in individual size due to either growth of sub-adult toads over time or disappearance of smaller individuals. However, there was a difference in size increases between Calvert Hills and Townsville. At Calvert Hills, sub-adults demonstrated an overall increase in mean body size from the early-wet through to the late-dry season, while at Townsville the increase commenced a season later, during the middle-wet, and continued through to the following early-wet season. Size frequency distributions (Figure 5.1) show these cohort fluctuations. The

difference between locations is probably due to a slower rate of growth by sub-adult toads at Townsville, due to lower temperatures, as well as density-dependant factors (see Chapter 4). Alternatively, variation in the timing of breeding seasons at Calvert Hills and Townsville may result in lack of synchrony of mean size of sub-adult cohorts. This appears unlikely because the seasonal mean size increases of juvenile toads do not differ between the localities increasing through successive seasons from the middle-wet to the following early-wet season. Although juvenile populations at both Calvert Hills and Townsville show this trend, the mean size increases are not as large at Townsville. Again, this may be a result of slower growth rates exhibited by non-adult toads at Townsville.

5.5 Summary.

The activity of toads within 10 metres of a water source varied between seasons and locations. Several factors such as site differences, climatic variation, hydric pressures and quality and quantity of retreat sites may have influenced toad activity at each location.

Site differences may have accounted for a higher number of active toads at Townsville than at Calvert Hills. Toads at Townsville sites were generally congregated around isolated dams whereas toads at Calvert Hills were distributed more evenly along river banks. The majority of toads congregated around dams at Townsville were males. Although this biased ratio occurred at both locations, it is thought that, due to more favourable climatic conditions, toads at Townsville may have a more protracted breeding season and males spend more time at the water's edge to maximise their breeding opportunities. Females, on the other hand, only come down to the water's edge if gravid or their hydric pressures are extreme. Juvenile recruitment into the Townsville toad population occurred over a longer time period compared to Calvert Hills. The harsher

climate at Calvert Hills reduced the time of the breeding season and the influx of juveniles into the population was correspondingly shorter. After 1-2 months of dry hot conditions at Calvert Hills, toads of all sizes and age categories came down to water to rehydrate Furthermore, during the dry season, when temperatures became cooler, toads became less active and probably remained within their retreat sites. It is during this time when mortality was high, especially amongst smaller toads. With slightly more favourable conditions at Townsville (ie. more dry season rainfall) toad mortality and inactivity appears to be not as pronounced.

The size of toads also varied considerably between seasons at each location. Female size was larger than males and is probably related to fecundity. The change in size of non-adults from one season corresponded to growth increments and mortality of smaller individuals during the dry season. Toads were generally larger during the wet season when food availability was high and breeding individuals were frequently encountered. It is also possible that only the largest, and therefore the fittest, toads survive through the dry season to the following wet season.

Chapter 6. Body Condition.

Abstract

Body condition, ($^3\sqrt{}$mass)/size, was shown to be a reliable indicator of a toad's overall condition and was therefore examined and compared between toad populations at Calvert Hills and Townsville. Body condition reflects the overall physical fitness of a toad and was shown to increase during the wet season and decrease during the dry season. The body condition of male and female toads responded differently to seasonal effects with females having more pronounced decreases and increases compared to males. These differences are suggested as being due to behavioural differences between the sexes with females investing energy reserves into breeding during the wet season. Juvenile toads also demonstrated relatively good condition for most seasons possibly due to a heavy investment into growth. However, when conditions become difficult from lack of food and harsh climatic conditions, the condition of juveniles declined severely. Although all age categories were shown to markedly decline, the timing of this decline varied between Calvert Hills and Townsville. At Calvert Hills this decline was noted late in the dry season corresponding to a period of extremely dry and hot conditions. Once early wet season rains commenced, and hence food supplies increased, toad condition improved. A decline in body condition, and subsequent improvement with favourable conditions, occurred a season later at Townsville. Dry season rain and variation in the timing of food availability may best explain these differences. Differences in body condition also occurred between sites and is proposed to be caused by differences in food and shelter availability and/or high numbers of toads active causing increased competition for these resources. An overall increase in toad body condition during the study period at Townsville may be correlated with a decreasing patterns of activity at this location.

6.1 Introduction.

Body condition is a reflection of the relationship between an animal's length and weight and may indicate an animal's general physical fitness. Animal populations with high body condition indices are usually more fit than those with lower body condition indices. This is also true for most anurans. Fluctuations in body condition of toads, for example, are thought be due to food availability, seasonal changes in body water content as well as differences in climate and habitat and breeding cycles.

Individual toads in high density populations are often in poorer condition than toads in low density areas (Denton and Beebee 1993a). For example, the body condition of *Bufo calamita* was inversely correlated to population density (Denton and Beebee 1993a). Toads from Townsville have been shown to have smaller body sizes and were in poorer body condition than toads in the Gulf of Carpentaria leading to an overall population decline(Freeland 1986; Freeland *et al.* 1986a; Freeland *et al.* 1986b). Freeland *et al.* (1986a) further suggested that food shortage may lead to poor condition in *B. marinus* populations particularly in the dry season. However, it may be a combination of water stress and food availability (Alford *et al.* 1995). Dietary differences for instance, explained the smaller size and emaciated condition of savannah populations of *B. marinus*, compared to rainforest toads that were larger and heavier (Zug *et al.* 1975). Similarly, body weight, an indicator of body condition in *B. calamita*, is directly related to food intake and availability (Denton and Beebee 1993a).

Toad body condition can also be influenced by seasonal fluctuations of body water content (Ryser 1989). Desiccation and absorption of water play an important part in determining the body weight of amphibians. The body weight of *B. marinus* is made up of approximately 76% water (Zug and Zug 1979), and toads are able to lose 52% of their water content before they die (Krakauer 1970). Therefore, differences in climate and

habitat between populations may also be responsible for variation in toad weight and condition. Other studies have shown that variation in weight for a given length is related to season (Chapman and Chapman 1958; Alford *et al.* 1995).

Increases and decreases in the body weight of toads are probably related to the greater abundance of food during the wet season and an increased water loss in the dry season. In tropical Australia, food availability, especially termites, is highest during the wet season, while harsh, dry environmental conditions in the dry season cause a decline in food availability. The body condition of *B. marinus* would therefore be expected to decline progressively from the end of the wet season.

Although variations in body condition arise from local environmental conditions, considerable variation also occurs during the breeding season (Jørgensen *et al.* 1986). A reduction in body mass within both males and females during and immediately after a breeding season has been demonstrated in numerous studies (Chapman and Chapman 1958; Durnham and Bennett 1963; Gibbons and McCarthy 1984; Jørgensen *et al.* 1986; Given 1988). Female *B. marinus* invest heavily in reproductive output (Hearnden 1991), and their body condition would be expected to decrease immediately after oviposition.

There is the possibility that changes in toad body condition may be a reflection of their total bladder water content which can account for up to 50% of a toad's total body weight (Krakauer 1970). Recent rainfall events may therefore increase a toad's body condition and, combined with the ability of *B. marinus* to rapidly absorb moisture from the soil (Zug and Zug 1979), may better account for variations in a toad's length to weight relationship.

In addition to examining several factors that may result in changes in toad body condition, including variations in site, season, and environmental variables such as rainfall,

this chapter will also examine whether recent rainfall significantly influences a toad's total body weight and condition. The effects of environmental factors on body condition are examined for male, female, sub-adult and juvenile *B. marinus* populations at Calvert Hills and Townsville. Furthermore, differences between these two regional populations are described and discussed.

6.2 Methods.

6.2.1 Body Condition.

Individual toad's body condition was measured using the formula:

$$\textbf{BODY CONDITION} = \sqrt[3]{\textbf{MASS}}/\textbf{SVL}$$

To determine if the above formula represents isometric growth (ie. $\beta = 3$) and is suitable for use in analysis in this chapter, a regression analysis was performed on the data. Using 95% confidence limits from the regression of length by weight it was shown that β encompasses three at both locations. For toads at Calvert Hills the 95% confidence limits for β are 2.987 to 3.193, while for Townsville toads the 95% confidence limits for β are 2.963 to 3.092. The relationship between lengths and weight at both locations is therefore isometric and the above formula is therefore valid for use in analysis.

Individual toad mass, calculated to the nearest 0.5 gram, and SVL (mm) were measured for every toad collected on every sampling night at Calvert Hills and Townsville (see sections 4.2.2 and 4.2.3). All toads were generally weighed before any voiding of their bladder content to minimise bias. Toads which did void their bladder content prior to

weighing were eliminated from this section of the study. Once calculated, body condition was transformed to body condition x 100, and is therefore referred to as body condition index (BCI), for ease of discussion and plotting.

To determine if age category, site and season, or any interaction of the three, affected toad body condition at either Calvert Hills or Townsville the data for each location were analysed separately using a three-factor ANOVA with replication.

Many sample sizes within this study were small and it is worth noting that Roth and Ráb (1987) recommended that small sample sizes, where $n \leq 5$, are insufficient to eliminate the effect of natural variability. Due to unbalanced data sets, type III sum of squares were used. All statistical analysis were performed using SAS 6.04 (SAS Institute 1995).

6.2.2 Effects of Rainfall on Body Condition.

The data were analysed using a maximum r-square multiple regression analysis to determine the relationship of:

a. elapsed time since a previous rainfall event;
b. the average amount of rain per day during that rainfall event; and
c. the length of time of the rainfall event, on male and female BCI

A major rainfall event was arbitrarily determined to have commenced when at least 25mm of rain fell on a single day. The event was deemed to have ceased when no daily rainfall exceeded 25mm for 30 days. The number of days between these periods was the length of a rainfall event. Average rain per day was calculated by dividing the number of days of the rainfall event by the amount of rain recorded. A previous rainfall event is

equivalent to the rainfall experienced during a wet season, while the average rain per day and length of rain event indicate the strength and duration of a wet season. The time elapsed since a rainfall event indicates the time since wet season rain ceased.

The criteria for a major rainfall event and previous rainfall were determined using rainfall records from each locality (Appendix 3). Calvert Hills rainfall was taken from Calvert Hills Homestead (January 1986 to May 1989, and January 1991 to June 1992) and Wollogorang Homestead (June 1989 to January 1991). Townsville rainfall records were obtained from the Townsville Bureau of Meteorology situated at Townsville airport (January 1986 to June 1993).

A linear regression was also performed to determine the relationship of recent rainfall up to three days prior to a toad's capture and weighing to adult toad BCI. This analysis was included to address the possibility that the calculated toad BCI is a reflection of bladder content and not overall condition.

6.2.3 Sex and Trip Effects on BCI.

To determine if body condition varied with sex (males and females) or trip (ie. a sampling event within a particular season including all sites and replicates) the data were analysed using a two-factor ANOVA with replication calculated separately for each location, Calvert Hills and Townsville.

Statistical analysis were performed using SAS 6.04 (SAS Institute 1995), using type III sum of squares due to unequal replication.

6.3 Results.

6.3.1 ANOVA on Body Condition.

The results from the three-way ANOVA of age category, site and season on toad body condition at both Calvert Hills and Townsville are summarised in Table 6.1. All factors and interactions were significant at Townsville except age category, while at Calvert Hills factors except site, and site by age category interactions were significant.

Table 6.1. ANOVA results for toad body condition against site, season and age category at Calvert Hills and Townsville. (* = significant at 0.05 level).

Season	**Calvert Hills**				**Townsville**			
	d.f.	**MS**	**F**	***P***	**d.f.**	**MS**	**F**	***P***
Site	1	1.30×10^{-5}	2.22	0.1364	2	1.05×10^{-4}	26.98	0.0001*
Season	4	1.74×10^{-4}	29.82	0.0001*	4	8.40×10^{-4}	227.7	0.0001*
Age Category	3	4.89×10^{-5}	5.88	0.0001*	3	1.03×10^{-5}	1.7	0.0594
Season*Age Category	12	2.15×10^{-5}	3.67	0.0001*	12	7.41×10^{-5}	18.89	0.0001*
Site*Season	4	3.44×10^{-5}	8.36	0.0001*	8	7.53×10^{-5}	18.74	0.0001*
Site*Age Category	3	3.11×10^{-6}	0.53	0.6609	6	1.23×10^{-5}	3.37	0.0069*
Site*Season*Age Category	12	1.34×10^{-5}	2.29	0.0066*	24	7.36×10^{-6}	1.88	0.0001*
Error (Residual)	4628	5.85×10^{-6}	-	-	10120	4.15×10^{-6}	-	-

Although variations between the early-wet, middle-wet, late-wet/early-dry and middle dry season were small, toad BCI was generally highest at Calvert Hills in the middle-dry season and lowest in the late-dry season. At Townsville, toad BCI varied little

between the middle-wet, late-wet/early-dry, middle-dry and late-dry season. The lowest mean toad BCI however, occurred in the early-wet season.

6.3.2 Highest Order Interaction.

Although several effects and interactions were significant in the ANOVA only the highest order interaction (ie. site by season by age category) is presented as it best describes the significant relationships of toad BCI at both locations.

The interaction of site by season by age category was significant for both locations (Table 6.1). Mean BCI of male, female and juvenile toads at Homestead were significantly higher than at Big Calvert River during the early-wet season (Figure 6.1). A significant interaction effect was difficult to determine for Townsville sites (Figure 6.2), but may be due to higher mean BCI for all age categories at Bell's Dam during the middle-dry season when compared to Bentley Lagoon and Rock Road Dam.

Figure 6.1. Mean BCI of toads in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry seasons at Calvert Hills sites. (Dashed horizontal line represents BCI (x 100) = 4.50 to better illustrate trends; standard errors and sample sizes are included).

Big Calvert River = ●, solid line;
Homestead = ▲, dashed line.

a) Males;
b) Females;
c) Sub-adults;
d) Juveniles.

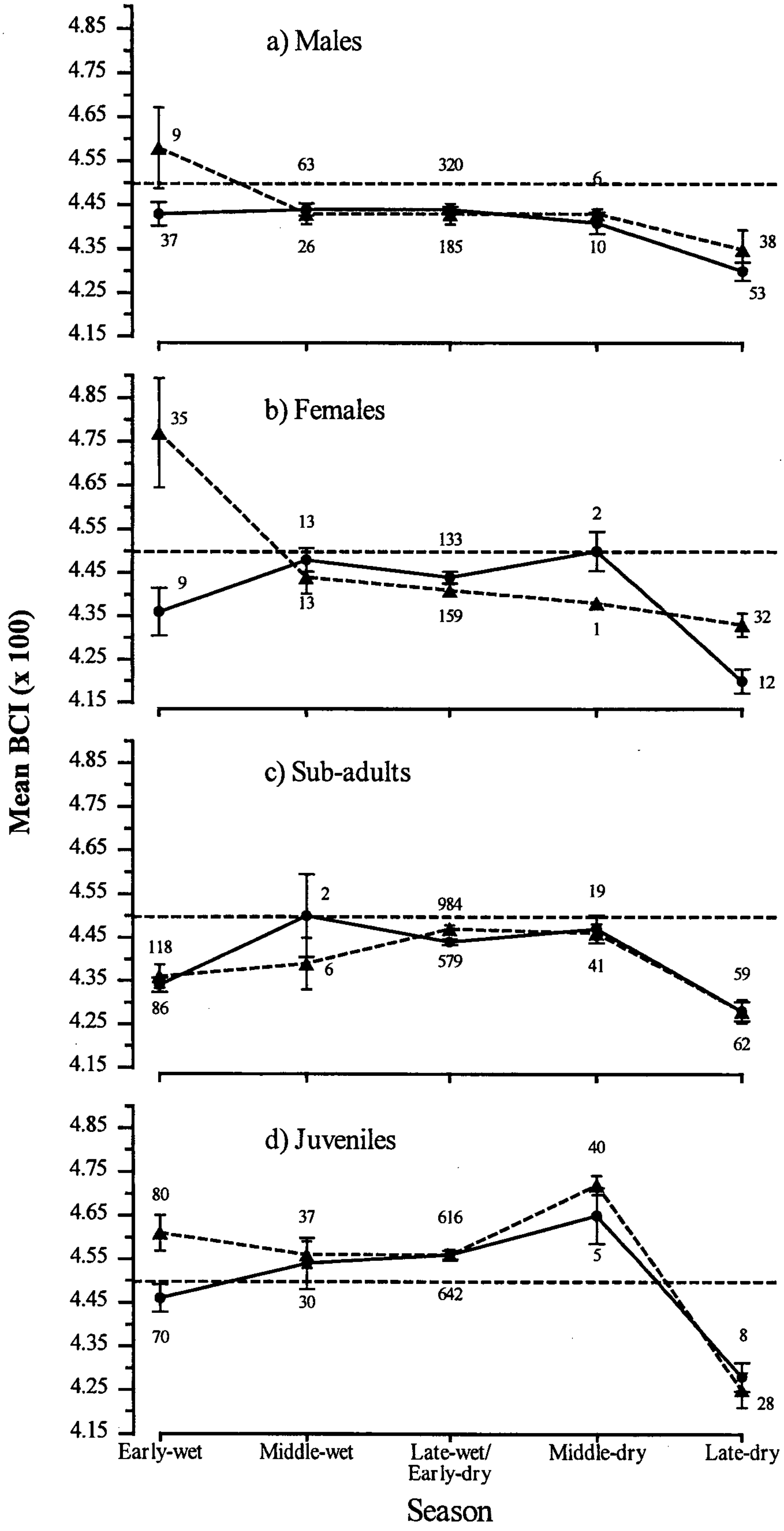
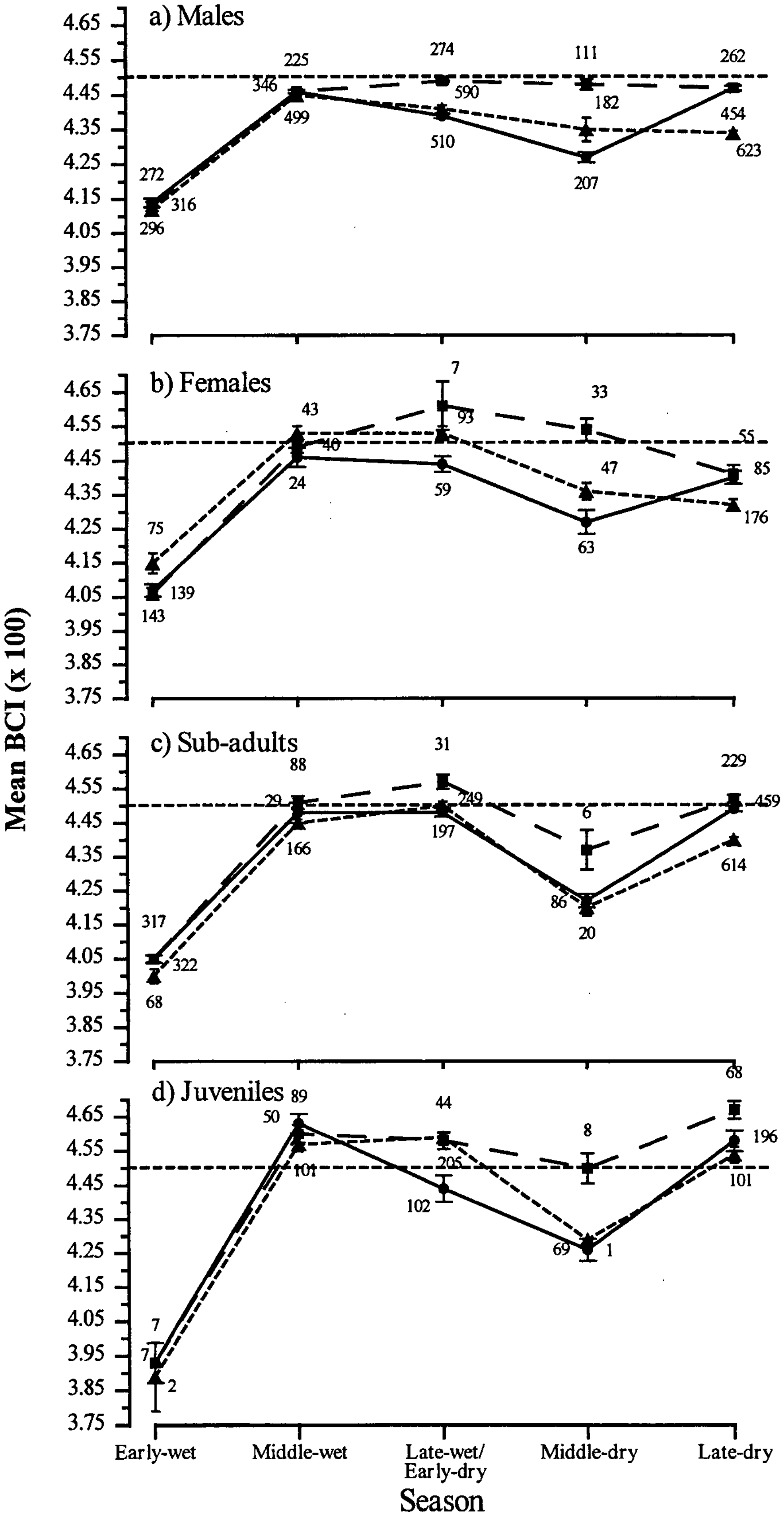

a) Males
b) Females
c) Sub-adults
d) Juveniles
Mean BCI (x 100)
4.85
4.75
4.65
4.55
4.45
4.35
4.25
4.15
9
63
320
6
37
26
185
10
38
53
35
13
133
2
9
13
159
1
32
12
2
984
19
118
6
579
41
59
86
62
80
37
616
40
5
30
642
70
8
28
Early-wet
Middle-wet
Late-wet/ Early-dry
Middle-dry
Late-dry
Season

Figure 6.2. Mean BCI of toads in the early-wet, middle-wet, late-wet/early-dry, middle-dry and late-dry season at Townsville sites (Dashed horizontal line represents BCI (x 100) = 4.50 to better illustrate trends; standard errors and sample sizes are included).

Bentley Lagoon = ●, solid line;
Rock Road Dam = ▲, short dashed line;
Bell's Dam = ■, long dashed line).

a) Males;
b) Females;
c) Sub-adults;
d) Juveniles;


Mean BCI (x 100)
a) Males
4.65
4.55
4.45
4.35
4.25
4.15
4.05
3.95
3.85
3.75
225
274
111
262
346
590
182
499
454
510
623
207
272
316
296
b) Females
7
33
43
93
55
40
47
85
24
59
176
75
63
139
143
c) Sub-adults
31
88
229
29
249
459
6
166
197
614
86
20
317
322
68
d) Juveniles
89
44
68
50
8
196
205
101
101
102
69
1
7
7
2
Early-wet
Middle-wet
Late-wet/ Early-dry
Middle-dry
Late-dry
Season

6.3.3 Rainfall Effects on Adult Toad BCI.

Positive or negative correlations as found by using a maximum r^2 multiple regression on the BCI of adult toads against rainfall factors are presented in Table 6.2. The statistics from this regression are presented in Appendix 12.

Table 6.2. Correlations (+ = significant positive correlation; – = significant negative correlation; blank boxes = no significant correlation), between adult toad BCI and rainfall variables for Calvert Hills and Townsville. (Shaded boxes indicate the same results for each locations).

	Calvert Hills		**Townsville**	
	Males	**Females**	**Males**	**Females**
Average Rain per Day	+		–	–
Length of Rain Event	–		+	+
Time Elapsed Since Event	–	–	–	–
r^2 (%)	**6.2**	**14.1**	**18.4**	**28.8**

For both Calvert Hills and Townsville adult toads lost body condition as the time since the last rainfall event increased (time since wet season rains). At Calvert Hills body condition increased for males with higher average rain per day during the wet season, but condition decreased with a longer wet season. However, at Townsville body condition decreased in male and female toads with more average rainfall per day in the wet season, but increased with a longer wet season duration.

The results of a linear regression using rainfall up to three days prior to adult toad capture and subsequent weighing are presented in Table 6. 3. No significant relationship was shown between adult toad BCI at Calvert Hills. For Townsville toads, a positive relationship was shown between male BCI and recent rainfall while a negative relationship was shown between female BCI and recent rainfall. Although significant, these relationships were weak with only 5% for males and 17% for females of the variation explained by the regression.

Table 6.3. Correlations (found via a linear regression) of rainfall up to three days prior to capture and weighing with male and female BCI at Calvert Hills and Townsville.

	Coefficient	r^2	t	Sig.
Calvert Hills				
Males	-5.1×10^{-6}	0.001	-0.722	0.471
Females	2.5×10^{-5}	0.003	1.181	0.238
Townsville				
Males	1.4×10^{-5}	0.05	5.075	0.000*
Females	-1.4×10^{-4}	0.17	-4.365	0.000*

6.3.4 Variation in Adult Toad Body Condition.

The results from the two-way ANOVA of sex (male & female) and trip on adult toad body condition are summarised in Table 6.4. Trip (or the date at which the sample was taken), and the interaction between trip and sex, were significant at both locations.

Table 6.4. Results of a two-way ANOVA on the effects of major sampling trips and sex on adult toad body condition at Calvert Hills and Townsville. (* = significant at 0.05 level).

	Calvert Hills				**Townsville**			
	d.f.	**MS**	**F**	***P***	**d.f.**	**MS**	**F**	***P***
Trip	11	8.45×10^{-5}	45.02	0.0001*	21	3.96×10^{-4}	153.9	<0.0001*
Sex (Males & Females)	1	2.90×10^{-7}	0.16	0.6925	1	2.22×10^{-6}	0.86	0.3533
Trip*Sex	11	1.26×10^{-5}	6.71	0.0001*	20	1.17×10^{-5}	4.54	0.0001*
Error (Residual)	1166	1.88×10^{-6}	-	-	6111	2.57×10^{-6}	-	-

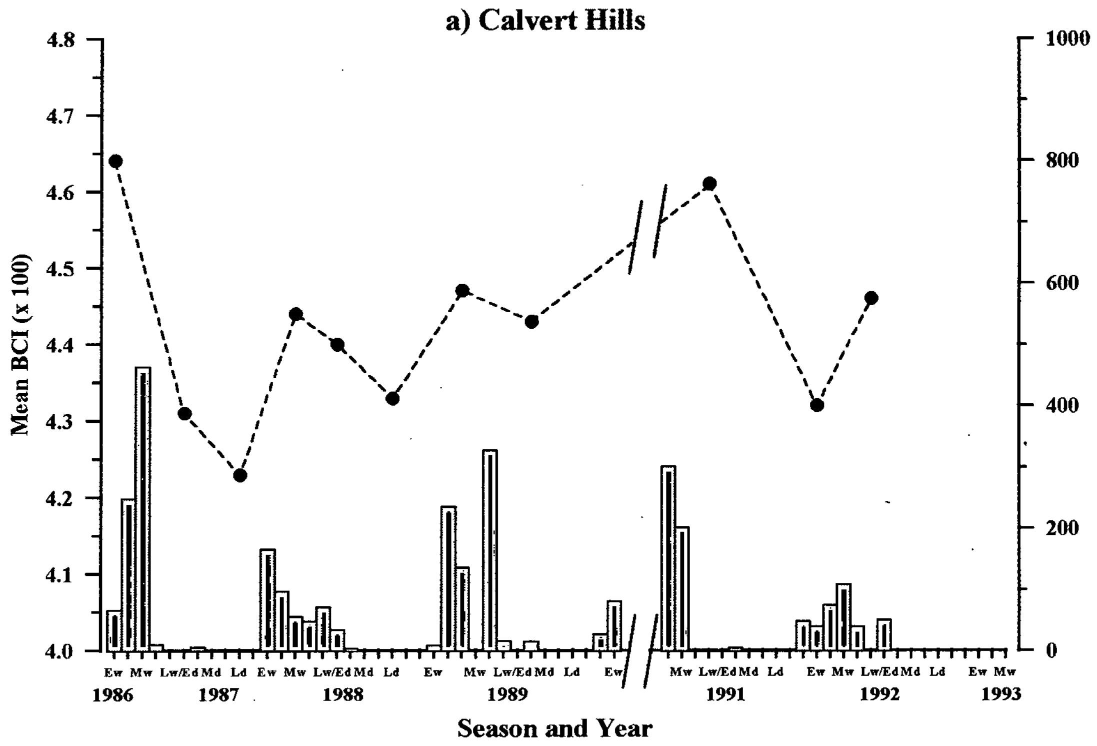
6.3.4.1 Trip Effects.

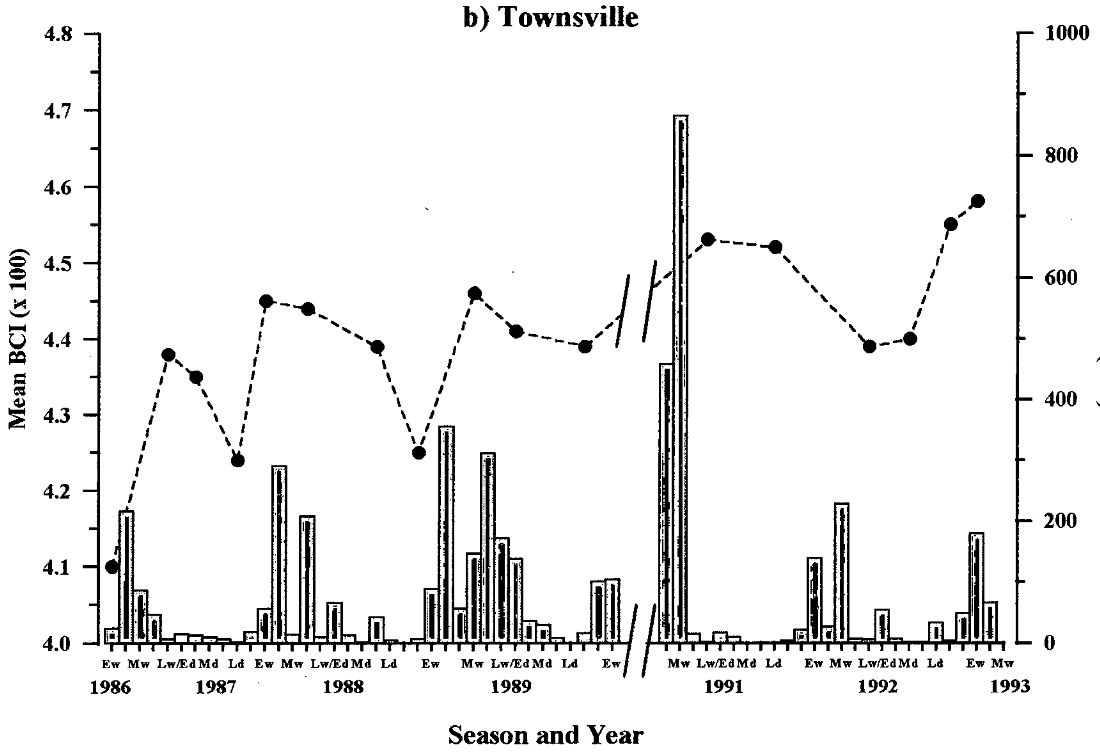
Trip had a significant effect on mean BCI. The mean BCI of adult toads at each sampling trip at Calvert Hills and Townsville, overlayed on monthly rainfall during the study period, is illustrated in Figure 6.3. Adult toad body condition generally improved at both locations after major rainfall events (ie. the wet season) and then decreased during periods with low or zero rainfall.

Figure 6.3. Mean adult BCI for each sampling trip (●) between 1987 to 1992 (excluding 1990). Monthly rainfall at Calvert Hills (red) and Townsville (blue) is also shown over this period. Season per trip is shown below the x-axis.

Ew = Early-wet,
Mw = Middle-wet,
Lw/Ed = Late-wet/early-dry;
Md = Middle-dry;
Ld = Late-dry.

a) Calvert Hills;
b) Townsville.


a) Calvert Hills
Mean BCI (x 100)
4.8
4.7
4.6
4.5
4.4
4.3
4.2
4.1
4.0
Rainfall (mm)
1000
800
600
400
200
0
Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw
1986 1987 1988 1989 1991 1992 1993
Season and Year


b) Townsville
Mean BCI (x 100)
4.8
4.7
4.6
4.5
4.4
4.3
4.2
4.1
4.0
Rainfall (mm)
1000
800
600
400
200
0
Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw Lw/Ed Md Ld Ew Mw
1986 1987 1988 1989 1991 1992 1993
Season and Year

6.3.4.2 Trip by Sex Interaction.

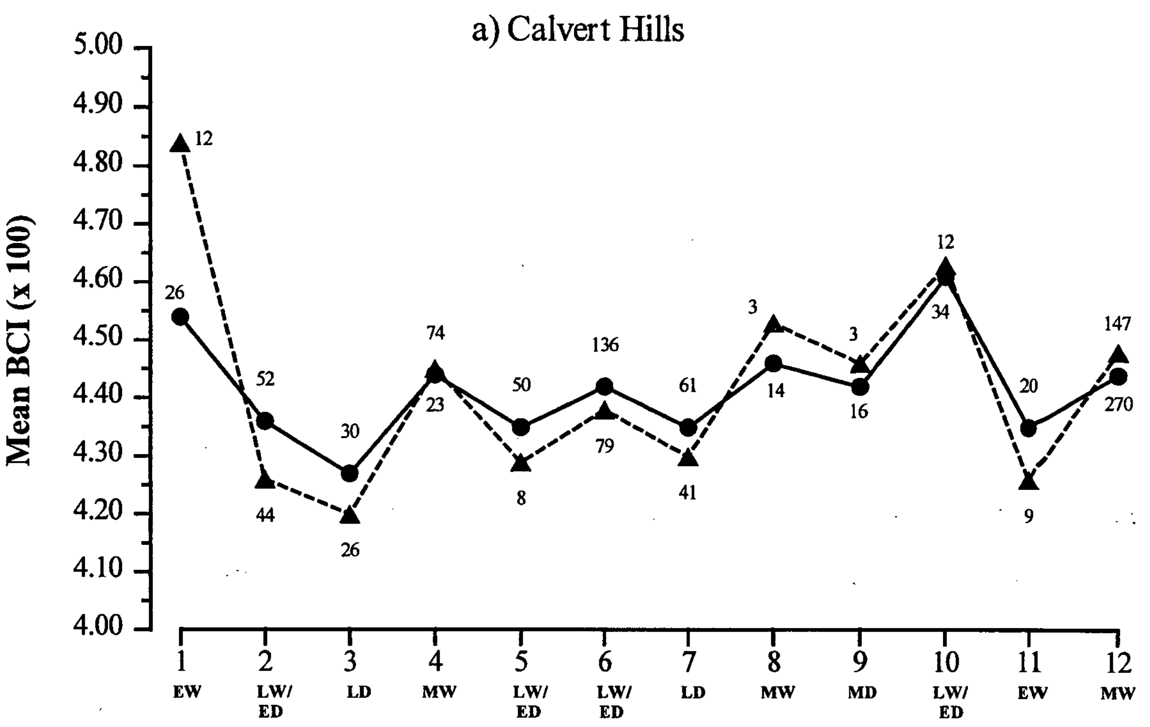
Male and female BCI for each sampling trip at Calvert Hills and Townsville is illustrated in Figure 6.4. Although the effect of sex was not significant at either location, there was significant variation in BCI between sex and trip. An increase in male and female BCI at Calvert Hills generally corresponded with wet season trips, while decreases corresponded with dry season samples (Figure 6.4a). When mean body condition was high, female BCI was often highest. However, when mean body condition was low, female condition was often lowest, ie. a reversal in female body condition occurred. That is, when conditions were good, females did better, but when conditions declined, females did worse when compared to males.

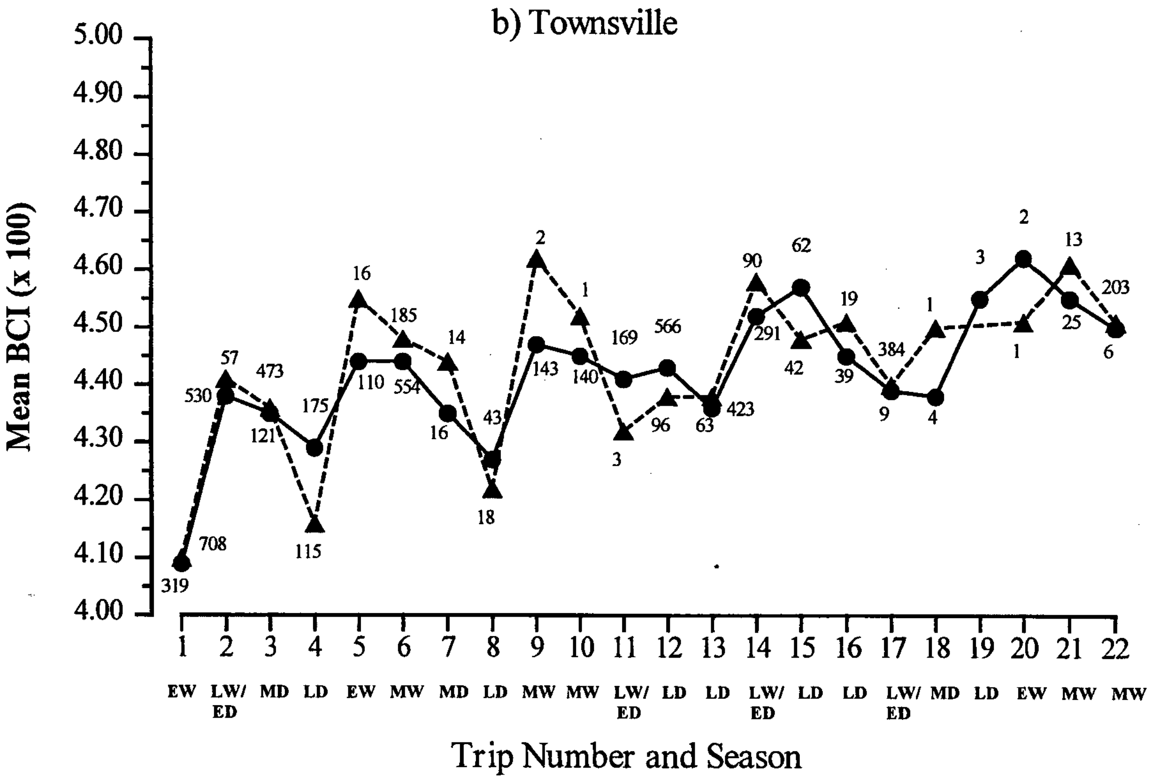
A similar overall trend was also apparent at Townsville (Figure 6.4b). Male and female body condition was generally higher during wet season trips and lower during dry season trips. As at Calvert Hills, when mean body condition was high at Townsville, female BCI was often highest, and when mean body condition was low, female BCI was lowest. An increasing trend in overall adult toad BCI from the commencement through to the end of the study was shown at Townsville.

Figure 6.4. Mean BCI per trip for males (●, solid line) and females (▲, dashed line). Season per trip is shown below the x-axis. (Sample sizes are included).

EW = Early-wet,
MW = Middle-wet,
LW/ED = Late-wet/early-dry;
MD = Middle-dry;
LD = Late-dry.

a) Calvert Hills;
b) Townsville.


a) Calvert Hills


b) Townsville

6.4 Discussion.

Although the calculated body condition may be indicative of an toad's overall fitness, the volume of bladder water of up to 50% of their total body weight (Krakauer 1970) may also account for much of the demonstrated variation in body condition shown during this chapter. It was therefore important to determine if changes in toad body condition were directly related to recent rainfall, and therefore a weight increase due to a higher amount of water stored in the bladder, or whether the BCI used during this chapter was indicative of the variance shown in the body condition of toads due to fluctuations in muscle or fat body content.

The regression analyses shown in Table 6.3 demonstrated that a strong positive relationship was not shown between toad BCI and rainfall up to three days prior to capture and subsequent weighing. This indicates that the seasonal variation in toad body condition shown throughout this chapter was probably not due to increases in toad body weight by storing more water in their bladder after recent rainfall. However, toads have capacity to absorb water from their surroundings such as moist soil via a thin ventral patch of skin (Shoemaker *et al.* 1992). This physiological response to hydration may therefore increase a toad's BCI by increasing weight via their total bladder content. The method of weighing toads after they had voided much of their bladder content probably eliminated some of the variation in BCI due to the weight of held bladder water. The BCI used for analysis throughout this chapter is therefore probably valid and is more likely to be a reflection of the toad's overall condition, ie. amount of muscle and fat body content, and not a response to an increased weight of the toad due to bladder water content.

The body condition of *B. marinus* during this study fluctuated according to seasonal conditions. For instance, body condition generally declined after rain periods such as the wet season at both Calvert Hills and Townsville. However, while toad body condition

increased during the wet season, the timing of these increases differed between locations. At Calvert Hills toad body condition peaked during the early- and middle-wet and then declined through to the late-dry season, while Townsville toads were in best condition during the middle-wet and declined through the dry season, before reaching its lowest level in the following early-wet season.

The observed differences in body condition between locations may have been caused by a number of different factors, but variation in climate between Calvert Hills and Townsville appears to be the most plausible explanation. Differences in climate leading to a decline in body condition may be related to severe hydric pressures placed on toads during extended dry periods, and a decrease in food supplies. With the onset of the wet season, an increase in prey abundance usually occurs (Zug and Zug 1979; Freeland and Kerin 1988), and food intake of all toads probably increase, resulting in an increase in energy reserves for breeding (ie. adult toads) and/or accelerated growth rates (ie. sub-adult and juvenile toads).

As the body condition of toads in Townsville showed a sharp increase a "season" later than at Calvert Hills, it is possible that food supplies were abundant earlier at Calvert Hills, and/or dehydration stresses were experienced later at Townsville. This was especially evident for males and females (Figure 6.4) where body condition clearly increased after wet season rainfall and decreased during the dry season.

Toads at Calvert Hills may respond quicker to favourable conditions compared to Townsville populations because of shorter rainfall periods characteristic of Gulf of Carpentaria wet seasons. Food may only be abundant for short periods from the commencement of the wet season. Due to the shorter wet season at Calvert Hills and the associated shorter time of peak food supplies, toads at this location must rapidly increase their body condition. Termites, for example, are abundant throughout Calvert Hills, and

usually swarm during this time (Anderson and Jacklyn 1993). Although similar food supplies exist at Townsville, they may not have been available until later in the wet season with more consistent rainfall. In addition to a longer wet season, Townsville also had more dry season rain during the study period and this may explain why body condition did not decline markedly until the early-wet season at this location. Sporadic rainfall during the early-wet season and Townsville, coupled with high temperatures (Oliver 1978), may have caused the sharp decline in toad body condition at this time. Dehydration stresses were also probably less severe in the dry season at Townsville as they were at Calvert Hills. The dry season was generally longer at Calvert Hills and the maximum diurnal temperature during this time were often over 35° C (see section 2.3.2). Toads that survive these environmental extremes through to the following wet season will probably lose body weight and therefore have a relatively lower body condition.

Marked seasonal variation in juvenile body condition, compared to other age categories, indicated that smaller toads were able to rapidly increase their body condition during favourable periods, ie. high food availability, but show a severe decline when conditions become very dry and harsh, and food supplies are limited. The body condition of juveniles also declined dramatically during the late-dry at Calvert Hills and the early-wet at Townsville but during other seasons they were generally in better condition than all other age classes. Toads at this stage probably spend as much time as possible feeding and exhibit rapid growth rates (see Chapter 4), and may have a better size to weight ratio than larger toads. That is, they require less food proportionally to larger toads before their body condition increases and this may be an adaptation to ensure rapid growth to the adult stage.

Females also demonstrated dramatic increases and decreases in body condition. Compared to males, the body condition of females showed marked variation, increasing after rainfall and decreasing during dry periods (Figure 6.4). During favourable conditions experienced during the wet season, female body condition was generally higher than that

of males, while after dry periods, females were in considerably poorer condition. Marked variation in the body condition of female toads is probably related to high amounts of energy lost during oviposition. Females spend the majority of their time foraging (van Beaurden 1978; Hearnden 1991) and can potentially rapidly increase their condition. The cost of foraging activity during this time is probably minimal in relation to the amount of food available. However, as a result of energy depletion due to the loss of eggs after breeding, female condition declines rapidly in relation to males during the wet season. Both male and female toads showed an improvement in body condition after rainfall and a decline after dry periods, the rates of improvement and decline varied between the sexes. Furthermore, variation occurred between male and female toads at Calvert Hills and Townsville in response to the length and degree of rainfall during the wet season.

Some site variation occurred at Calvert Hills and Townsville. Toad body condition at Homestead, especially that of sub-adults, was generally lower than at Big Calvert River during the early-wet and middle-dry season. A number of factors may have been responsible for this observed decrease in condition including a decreased food supply and fewer shelter sites. It is unlikely that a high number of toads active during a sample was the cause for this decline because toad activity was lower at Homestead than at Big Calvert River (Chapter 5).

An increasing trend in toad body condition at Townsville was recorded over the study period (Figure 6.3b) and probably corresponds to the decreasing trend in the number of toads active reported in Chapter 5. As the number of active toads decreases, density-dependant factors on food supply may decline and lead to an increase in overall toad body condition. On closer inspection, an increasing trend in toad condition may be due to variation between Townsville sites. For instance, toads at Bell's Dam were generally in best condition, while Rock Road Dam toads were in poorest condition. It has previously been shown that the number of toads active at Bell's Dam are lower than either Rock Road

Dam or Bentley Lagoon (Chapter 5). Therefore, with lower numbers of toads active, and subsequent lower rates of competition for food and shelter, toads at Bell's Dam may hold their body condition at higher levels, especially during the dry season, than at the other two Townsville sites.

6.5 Summary.

Toad body condition fluctuates markedly between seasons in the wet-dry tropics of northern Australia. During the wet season, when conditions are favourable, high food availability allows toads to increase their body condition. Juvenile toads in the wet season demonstrate rapid growth rates and have a corresponding high body condition. While juvenile body condition remains high into the dry season, their condition eventually worsens from harsh climatic conditions and lack of food towards the end of the dry season. Females also put considerable effort in foraging to build up energy reserves for breeding. However, after oviposition, the body condition of females declined either due to a decrease in fitness or a net loss in weight.

The timing of body condition declines and increases shows regional variation. Due to short wet seasons and prolonged dry seasons in the Gulf of Carpentaria, toad populations rapidly increase their condition at the commencement of favourable conditions, ie. early in the wet season, due to high food availability, and decline late in the dry season due to hot and dry conditions and a lack of food. Townsville populations maintain a high body condition through the dry season, which is relatively less harsh, and do not decline until the start of the wet season. High numbers of toads active at a site, and therefore less food per animal, may cause a reduction in the overall body condition of a toad population.

Chapter 7. Factors Affecting Diurnal Shelter Use.

Abstract

Patterns of diurnal retreat site use by 50 adult *Bufo marinus* were experimentally examined in a 45 m^2 enclosure containing 18 artificial shelters, nine each in its eastern and western halves. At 15 times (samples), each separated by 48 h, each toad was captured and its location within the enclosure recorded. The soil moisture and temperature under each shelter was also recorded. After data were taken, toads were released at the centre of the enclosure. There were five experimental treatments, each carried out over three consecutive samples: an initial unwatered treatment (U1), water applied with a hose to saturate the western half of the enclosure (W), a second unwatered treatment (U2), water applied to the eastern half of the enclosure (E), and a third unwatered treatment (U3). The watering treatments affected the distribution of toads within the enclosure; by the end of each watering treatment, many toads had switched to the watered half of the enclosure. Toad density under shelters increased with increasing soil moisture. When soil moisture was greater than zero, more toads were found under shelters with higher soil temperatures. Toads aggregated under shelters, suggesting that they preferred sites already occupied by other individuals. They also returned to the same shelter in consecutive samples more frequently than expected if shelter selection was random. Aggregation and shelter fidelity may serve to reduce effective surface area/volume ratios and may also allow toads to take advantage of increased soil moisture caused by individuals urinating in shelter sites.

7.1 Introduction.

Amphibian daily movements are related to obtaining food, shelter, and mates, and to regulating body moisture and temperature (Beshkov and Jameson 1980; Woolbright 1985). These objectives often conflict. Most amphibians have permeable skin and lose body water rapidly (Wygoda 1984, 1989; Shoemaker *et al.* 1992). Rapid dehydration is thus a major threat to amphibian survival when on land (Malvin and Wood 1991). One way to avoid water loss is to remain in water, in the vicinity of water, or in moist habitats away from water (Thorson 1955). Restriction of activity to such areas may interfere with thermoregulation, foraging, and other activities. One possible compromise is to select retreat sites for suitable moisture and temperature regimes and for their proximity to other resources, and to partition time between retreat sites and the pursuit of other resources in more hostile habitat.

B. marinus are widely distributed in seasonal tropical and sub-tropical regions in Australia (Freeland and Martin 1985). In these areas, free water is often scarce during the hot, dry summers, and the activity ranges of *B. marinus* are often limited by moisture availability. *B. marinus* is typical of the genus *Bufo* in its water relations; it loses water rapidly (Wygoda 1984), can tolerate large amounts of water loss (up to 50% of their body mass; Zug and Zug 1979), and has the ability to reabsorb water from the bladder, which can account for 25% of the body mass of a fully hydrated toad (Malvin and Wood 1991). Regular access to water for rehydration is essential to replace losses (Shoemaker *et al.* 1992). *B. marinus* rehydrates by absorbing water through a thin ventral pelvic patch of highly vascularized skin (Zug and Zug 1979; Shoemaker *et al.* 1992). Water can be absorbed from standing water or from damp soil. In tropical areas *B. marinus* is primarily nocturnal (Zug and Zug 1979), spending the daytime hours in retreat sites. Water limitation may make the selection and use of diurnal retreat sites a critical factor in its survival.

Little has been reported about diurnal retreat sites of toads or frogs. Dole (1965) reported that *Rana pipiens* cleared wet soil of dead vegetation with their hind feet. These bare patches were often surrounded on three sides by a ridge of dead grass (10-15cm high) resulting in "forms". Moisture ranges in "forms" were higher than in the adjacent habitat. Forms provided shelter and reduced water loss (Dole 1965). During the day *B. marinus* is generally inactive, sheltering under shallow plant litter on the ground (Jaeger and Hailman 1981), in burrows or depressions (Zug and Zug 1979), or in forms similar to those observed by Dole. The need to conserve moisture affects the toads choice of retreat sites (Smits 1984; Smits and Crawford 1984; Dobkin *et al.* 1989), and can interact with the need to choose an appropriate thermal environment (Crump 1986; Dobkin *et al.* 1989; Huey *et al.* 1989). The availability of suitable daytime retreats may limit toad density (Blair 1960; Stewart and Pough 1983).

Because retreat sites may be limiting and their quality may affect survival through the dry season, *B. marinus* is likely to show retreat site fidelity. It is known to home using both visual and previously learned topographic cues (Brattstrom 1962; Carpenter and Gillingham 1987). In addition, chapters 5 and 6 suggest that hydric requirements may limit toad populations especially during the dry season in the wet-dry tropics. One of these limiting factors may be the lack of suitable shelter sites. Characterstsics of suitable shelter sites are largely unknown and, once determined, may provide further support that hydric requirements are important for toad survival.

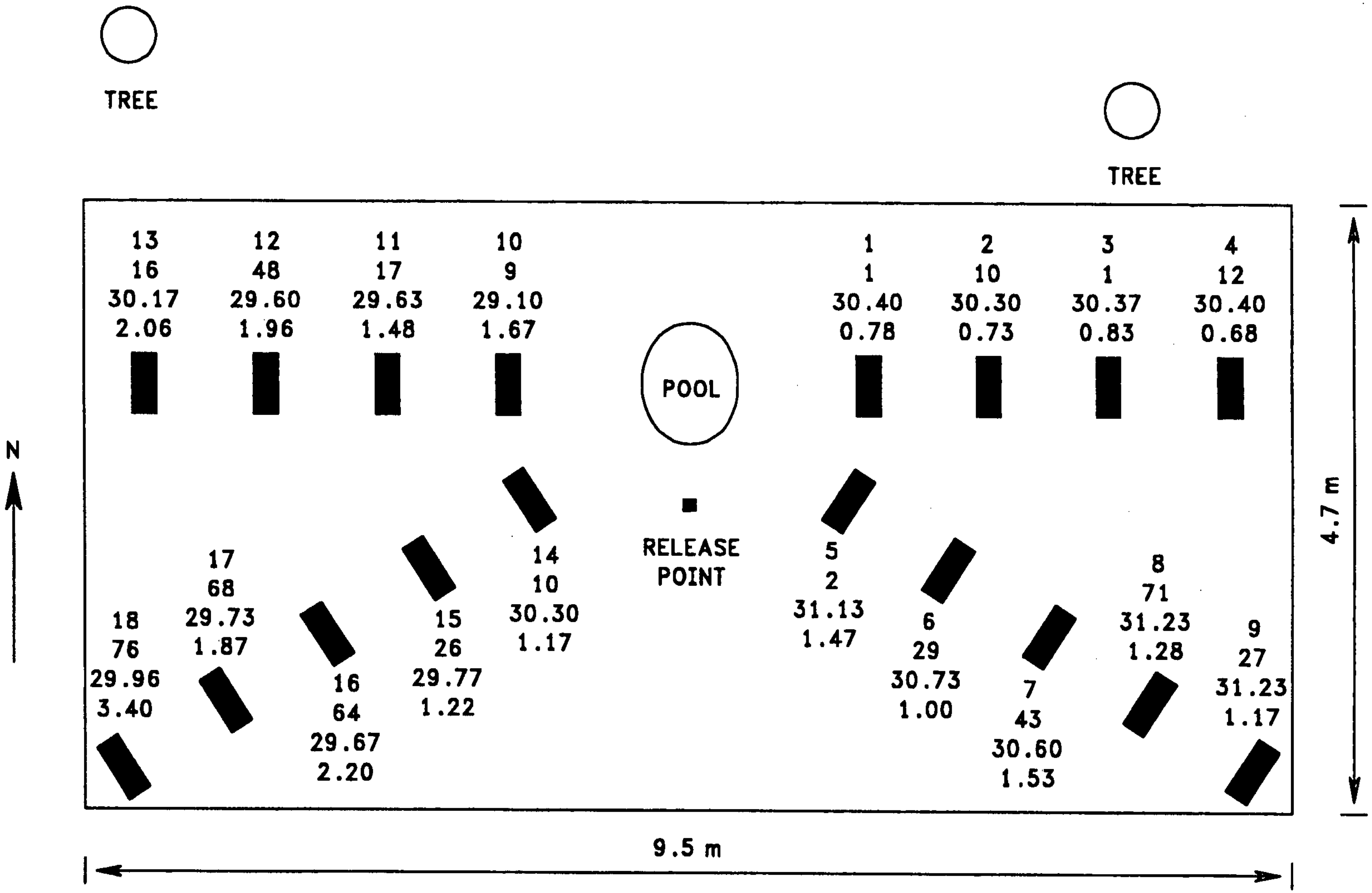
This chapter therefore investigates shelter site characteristic and reports the results of an experiment on retreat site selection and use by *B. marinus*. Artificial shelters and an experimental moisture regime were used to investigate how retreat site selection varies with temperature and soil moisture. The spatial distribution of toads among retreat sites and retreat site fidelity by individual toads were also examined.

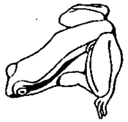
7.2 Methods.

7.2.1 Enclosure.

During October 1989, an enclosure (25 mm chicken wire, 9.5 m x 4.7 m x 1 m high; Figure 7.1) was constructed at James Cook University, Townsville, Queensland, Australia (Figure 2.1). Eighteen artificial shelters were positioned, each a longitudinally sectioned half of a 20 x 50 cm length of PVC tube, as shown in Figure 7.1. Parts of the enclosure were lightly shaded at some times by trees situated outside the northwest and northeast corners. A large tree at the northwestern corner provided a region of approximately 50% shade that extended from the northern edge of the enclosure to near the southern edge. The shadow entered the western edge of the enclosure at about 1030h and left the eastern edge at about 1530h each day. It encompassed most of the western third of the enclosure at noon. The shadow of a small bushy tree near the northeastern corner of the enclosure extended about 2m into the enclosure, providing approximately 40% shade to an area approximately 3 x 2 m at noon. Insolation was also affected by the shade from a stand of open forest 10m from the eastern edge of the enclosure, which caused a delay of approximately 55 minutes between the time the morning sun first struck the western edge of the enclosure and the time it reached the eastern edge. This light and shading regime caused shelters in the eastern half of the enclosure to warm more slowly in the morning and reach slightly higher temperatures than those in the western half (grand means of temperatures measured at time of sampling during the experiment: eastern shelters $\bar{x}$ = 30.71° C ± 0.26 SE, n = 135; western shelters $\bar{x}$ = 29.76° C ± 0.21 SE, n = 135; $t = 2.806$, $P = 0.0054$). Near the centre of the enclosure a small plastic pool (1 m in diameter x 20 cm deep) was sunk into the ground and filled with water. For the purposes of the experiment, the enclosure was considered to consist of eastern and western halves each with nine shelters.

Figure 7.1. Map of enclosure showing position of shelters (▬), pool, release site (■), and trees outside the fence. Numbers adjacent to shelters indicate (from top to bottom) shelter number, number of toad days spent under that shelter during the experiment, mean soil temperature at time of sample over the experiment, and mean soil moisture over the experiment.


TREE
TREE
13
16
30.17
2.06
12
48
29.60
1.96
11
17
29.63
1.48
10
9
29.10
1.67
POOL
1
1
30.40
0.78
2
10
30.30
0.73
3
1
30.37
0.83
4
12
30.40
0.68
N
RELEASE POINT
14
10
30.30
1.17
15
26
29.77
1.22
16
64
29.67
2.20
17
68
29.73
1.87
18
76
29.96
3.40
5
2
31.13
1.47
6
29
30.73
1.00
7
43
30.60
1.53
8
71
31.23
1.28
9
27
31.23
1.17
4.7 m
9.5 m



7.2.2 Sampling.

Fifty adults of *B. marinus*, 10 females and 40 males (selected to represent sex ratio usually encountered in the field), were weighed to the nearest 1g and measured to the nearest mm (size: $\bar{x}$ = 101.3 mm ± 7.38 SE, range 92-122 mm; weight: $\bar{x}$ = 95.02 g ± 3.28 SE, range 65-161 g). Each toad was individually marked by toe-clipping (see section 5.2.3). All toads were simultaneously released at the central point of the enclosure. The enclosure was subsequently checked every 48h during mid- to late-afternoon. At each check (sample), each toad was captured its location was recorded. At the end of each sample, all toads were simultaneously released at the central point of the enclosure (Figure 7.1).

7.2.3 Environmental Variables.

During each sample, several environmental variables under shelters were measured. These were maximum and minimum temperatures, relative soil moisture, and soil temperature. Maximum/minimum thermometers were placed under two randomly selected shelters in each half of the enclosure at the start of the experiment and after each sample. They were read and their location re-randomized at each sample. Relative soil moisture was read at a depth of 1 cm under each shelter using a conductivity meter. The meter was calibrated so that total saturation of the soil was equivalent to a reading of 10, while no moisture was equivalent to a reading of zero. The soil temperature was measured under each shelter at every sample by inserting a thermometer approximately 1 cm into the soil.

7.2.4 Treatments.

The experiment continued over 15 samples. Five treatments were applied during the experiment. These were no watering (treatment U1, U2 and U3), watered western half only (treatment W), and watered eastern half only (treatment E). Each treatment (U1, W, U2, E, U3) lasted through three consecutive samples. Watering involved thoroughly saturating the ground of one end of the enclosure with a hose for approximately 20 minutes every 48h after all toads were collected during a sample and before toads were released.

7.3 Results.

7.3.1 Toad Distribution Within the Enclosure.

Toads initially took some time to take advantage of the artificial shelters. During the first three samples (Treatment U1), only 82% of recovered toads were found under shelters. The remaining toads were discovered either under grass clumps (10%) or in the central pool (7%). The percentage of toads found under shelters increased during the other four treatments, never falling below 90%.

The distribution of the 50 toads within the enclosure during the experiment is summarized in Table 7.1. Each capture of an individual toad in a sample is counted as one toad-day. Toad-days were analysed as independent indicators of preference for shelters and areas of the enclosure because all individuals were released at the centre of the enclosure at the end of each sample; this forced them to select shelters and locations before each census. The treatments affected the distribution of toads between the western and eastern

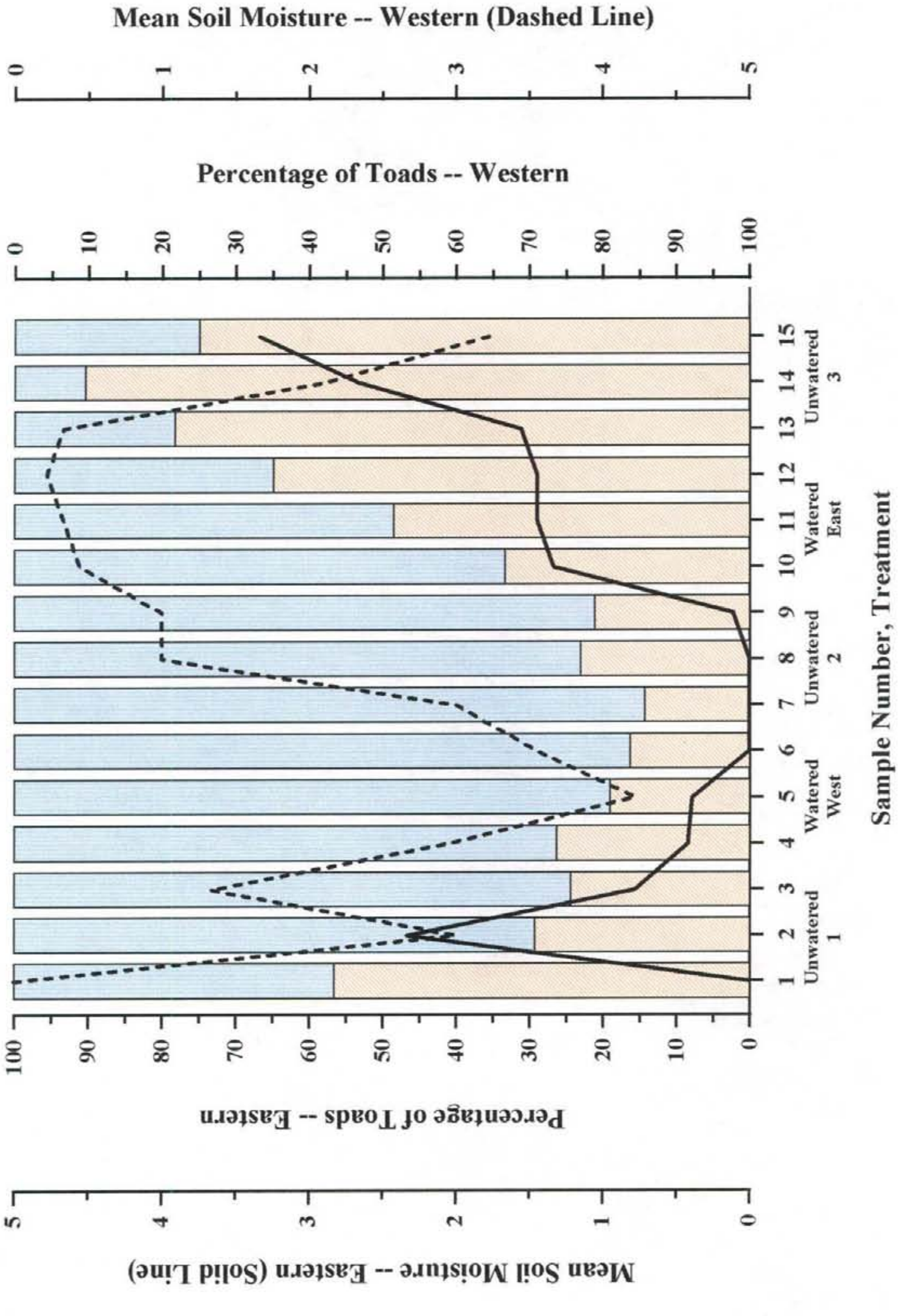
halves of the enclosure (contingency test, $\chi^2 = 97.52$, 4 df, $P < 0.0001$). The total number of toad-days across all treatments declined during the experiment because some individuals disappeared; presumably they either escaped or were removed by aerial predators.

The percentages of toads in the eastern and western halves of the enclosure at each census are shown in Figure 7.2, which also shows mean soil moisture under shelters in each half of the enclosure on each sampling date. Rainfall before samples 2 (ca. 10 mm), 14 (ca. 3 mm) and 15 (ca. 10 mm) raised soil moisture levels in both halves of the enclosure. At sample 1, toads were distributed nearly evenly between the eastern and western halves of the enclosure, which both had a mean soil moisture of 0. Rainfall between samples 1 and 2 increased the soil moisture in the western half of the enclosure to a mean reading of 3.00, while those in the eastern half increased to a mean of 2.33. During sample 3, the moisture of western shelters remained higher than that of eastern shelters (Figure 7.2). In samples 2 and 3, the distribution of toads became biased towards the western half of the enclosure.

Table 7.1. Summary of results of the experiment; number (and percentage) of toad-days found under shelters (east and west), in grass and in water, during each treatment. A toad-day is one toad in one sample.

Treatment	Number of Toad-days (%)			
	East Shelters	West Shelters	Grass	Water
Unwatered (U1)	39 (29)	73 (54)	14 (10)	10 (7)
Watered West (W)	25 (19)	98 (76)	3 (2)	3 (2)
Unwatered (U2)	23 (19)	96 (79)	2 (2)	0 (0)
Watered East (E)	53 (48)	55 (50)	2 (2)	1 (1)
Unwatered (U3)	59 (74)	14 (18)	4 (5)	3 (4)

Figure 7.2. Percentage of toads found in the eastern (red bars) and western (blue bars) halves of the enclosure at each sample and mean soil temperature in each half of the experiment during each sample.


Mean Soil Moisture -- Western (Dashed Line)
0
1
2
3
4
5
Percentage of Toads -- Western
0
10
20
30
40
50
60
70
80
90
100
Percentage of Toads -- Eastern
100
90
80
70
60
50
40
30
20
10
0
Mean Soil Moisture -- Eastern (Solid Line)
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Unwatered 1
Watered West
Unwatered 2
Watered East
Unwatered 3
Sample Number, Treatment

Once watering of the western half commenced, the number of toads on this side increased further (84% west at sample 6). The soil moisture on the western side remained relatively high and toads continued to favour this side (overall 81% west, 19% east) well into the next unwatered treatment (treatment U2). When the next watering treatment commenced (watering of the eastern half; treatment E) the soil moisture in the eastern half increased and toads shifted from the western to the eastern half (reaching 65% in the eastern half at sample 12). This shift continued during treatment U3, reaching a maximum of 90% of toads in the eastern half at sample 14. Rainfall then increased the moisture levels on both sides of the enclosure and the bias in toad distributions began to decrease in sample 15.

These patterns strongly suggest that the distribution of toads under shelters within the enclosure was related to soil moisture. The effects of watering thus persisted after watering ceased.

To investigate the effect of watering, the samples were divided into three groups:

a. unwatered, when that half of the enclosure had not been watered during the previous eight days;
b. watered, when that half of the enclosure was being watered; and
c. previously watered, when that half of the enclosure had been watered at least once during the previous eight days.

The mean numbers of toads recorded for the watered and previously watered groups of samples were approximately equal (watered: $\bar{x} = 25.17 \pm 3.85$ SE, n = 6 samples; previously watered: $\bar{x} = 25.83 \pm 3.563$ SE, n = 6 samples). The mean number of toads recorded during the unwatered samples was approximately half that of the other two treatments ($\bar{x} = 12.72 \pm 1.928$ SE, n = 18 samples). This indicates that toads favoured areas within the enclosure that were moist from watering or areas that remained moist after the watering treatment.

7.3.2 Effects of Soil Moisture.

More toads occurred under shelters with moister soil. The number of shelter-days at each relative soil moisture was calculated (Table 7.2). A relative soil moisture of zero (ie. dry soil) was the most common reading (101 shelter-days out of a possible 270). However, shelters with this soil moisture had the lowest rate of occupancy by toads (33.7%) and the lowest number of toads per shelter (0.71).

A chi-squared contingency test comparing the total number of shelter-days at a particular soil moisture with the number of toad-days spent in these shelters was significant ($\chi^2 = 73.45$, 5 df, $P < 0.0001$). This analysis suggests that toads selected shelters based on soil moisture, or that the presence of toads increased soil moisture, or some combination of these effects. The same analysis was performed with the zero class of soil moisture omitted. With this data set the number of toad-days per shelter-day still responded to soil moisture ($\chi^2 = 14.16$, 4 df, $P = 0.0068$). The data (Table 7.2) indicate that there was a general trend for increasing numbers of toads to occur under shelters with higher soil moisture.

Table 7.2. Responses of toads to relative soil moisture.

Soil Moisture	Total Number of Shelter-days	Number of Shelters with Toads Present (% of Shelter-days)	Total Number of Toad-days	Toad-days per Shelter-day
0	101	34 (34)	72	0.71
1	58	44 (76)	132	2.28
2	52	37 (71)	143	2.75
3	26	13 (50)	40	1.54
4	23	17 (74)	90	3.91
≥5	10	10 (10)	58	5.8

7.3.3 Effects of Soil Temperature.

Maximum and minimum air temperatures were available for 60 shelter-days, while soil temperature at the time of sampling was available for 270 shelter-days. Soil temperature at the time of sampling correlated well with the two-day maximum air temperature when it was available ($r = 0.64$, $P < 0.0001$). Soil temperature was therefore analysed at the time of sampling, allowing me to use data for all 270 shelter-days.

The analysis was complicated by the fact that soil temperature was affected by soil moisture. Soil temperatures ranged from 29 to 38° C under shelters with a soil moisture of 0, while shelters with a soil moisture greater than 2 experienced soil temperatures between 22 and 33° C. An analysis of covariance was used to separate the effects of moisture and temperature. Within each of six classes (0-5+) of soil moisture, the mean number of toad-days per shelter-day was calculated at each one-degree increment of temperature. This was used as the response, while moisture category was the classification

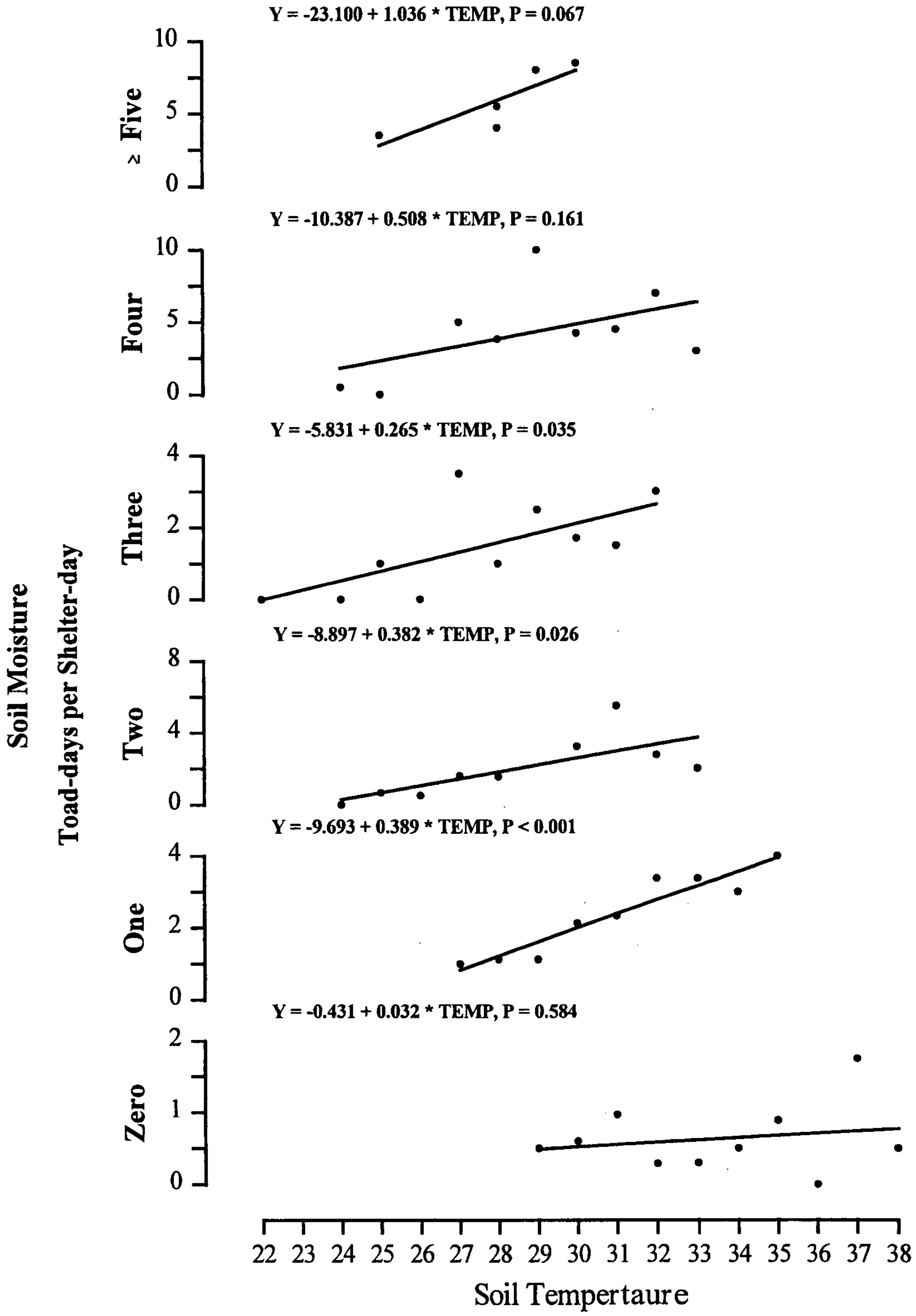
variable and soil temperature was the covariate. The analysis was performed using SAS 6.04 (SAS Institute 1995) with Type I sums of squares, with moisture introduced into the model first, temperature introduced second, and their interaction third. The hypothesis tests were constructed in this manner to examine the effects of temperature after removing the effects of moisture from the model, and to look for possible changes in the slope of the temperature response only after removing the main effects of temperature and moisture.

Soil moisture category significantly affected the number of toad-days per shelter-day ($F_{5,40} = 12.90$, $P < 0.0001$), as did soil temperature ($F_{1,40} = 21.52$, $P < 0.0001$). The interaction was not significant ($F_{5,40} = 1.69$, $P = 0.1592$), suggesting that all regressions had the same slope. The response of number of toad-days per shelter-day to soil moisture and temperature is illustrated in Figure 7.3. For all soil moistures greater than zero, toads tended to occur more often under shelters at higher temperatures. Although the interaction between soil moisture and soil temperature was not significant, the very small and non-significant relationship of shelter occupancy to temperature when the soil moisture was zero suggests that the preference for higher temperatures disappeared under very dry conditions.

7.3.4 Aggregation Under Shelters.

Shelters often contained more than one toad. Figure 7.4 compares the observed and (Poisson) expected numbers of shelter-days with different numbers of toads. A shelter-day is one shelter in one sample. A chi-squared test comparing the observed and expected numbers of shelter-days with 0 to >7 toads shows that many more shelter-days had zero toads or large numbers of toads than expected ($\chi^2 = 110.8$, 8 df, $P < 0.0001$). This demonstrates that the distribution of toads under shelters was aggregated.

Figure 7.3. Mean number of toad-days per shelter-day at each combination of temperature and soil moisture encountered during the experiment. Lines illustrate the least-squares regression shown for each soil moisture.


Y = -23.100 + 1.036 * TEMP, P = 0.067
Y = -10.387 + 0.508 * TEMP, P = 0.161
Y = -5.831 + 0.265 * TEMP, P = 0.035
Y = -8.897 + 0.382 * TEMP, P = 0.026
Y = -9.693 + 0.389 * TEMP, P < 0.001
Y = -0.431 + 0.032 * TEMP, P = 0.584
≥ Five
Four
Three
Two
One
Zero
10
5
0
10
5
0
4
2
0
8
4
0
4
2
0
2
1
0
Soil Moisture
Toad-days per Shelter-day
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
Soil Tempertaure

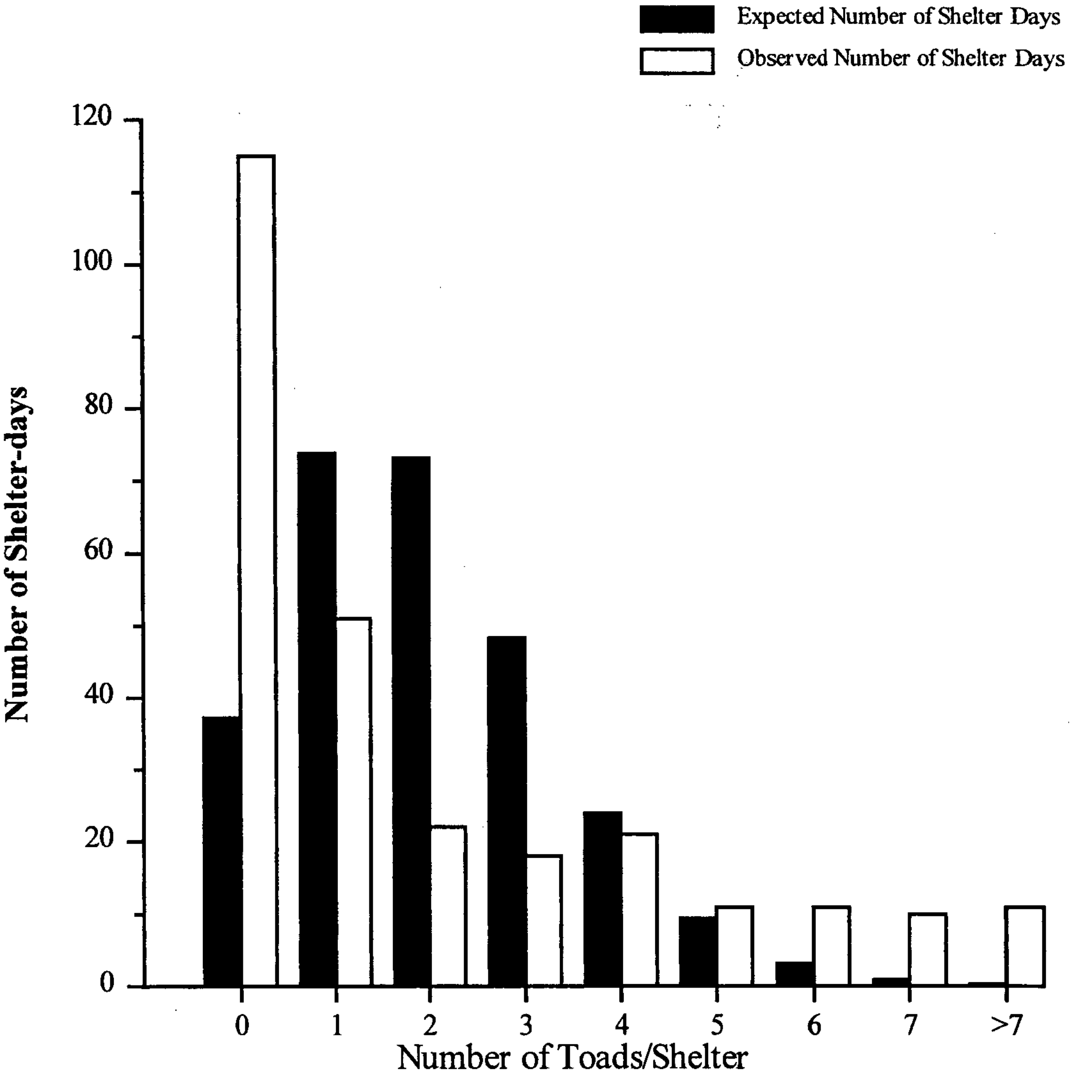


Figure 7.4. The number of shelter-days observed (filled bars) and expected (open bars) against the number of toads per shelter.

7.3.5 Favoured Shelters.

The wide variation in number of toad-days spent under shelters during the experiment (Figure 7.1) indicates that toads preferred certain shelters. Much of this preference may have been caused by a combination of shading and orientation affecting the temperature and moisture regimes of the shelters. Four of the six shelters that had the highest number of toad-days (> 40; shelters 7, 8, 12, 16, 17, and 18) were in the western third of the enclosure, which was shaded at midday. It also appears that shelters not oriented in a north-south direction attracted more toads. The average temperature of shelters in the western half of the enclosure on the nine sampling dates before the eastern half was watered was 32.1° C (SE = 0.64, n = 9), lower than that in the eastern half. This may account in part for the relatively high numbers of toad-days in the shelters in the unshaded southeast corner of the enclosure. These shelters had higher mean soil moisture than the north-south oriented shelters in that half of the enclosure (Figure 7.1). Their orientation may have reduced air movement and thus water loss; unfortunately, air movement was not measured. The six shelters with the lowest frequency of toads under them (10 or less) were all near the pool and experienced relatively high temperatures and low soil moisture on average (Figure 7.1). Five of these shelters received no shade near midday when the sun is most intense.

7.3.6 Fidelity to Shelters.

Individual toads were often found using the same shelter in consecutive samples (Table 7.3). A Monte Carlo computer simulation of 10,000,000 toads selecting among shelters on 15 consecutive samples was used to generate an expected distribution of numbers of consecutive captures in the same shelter. Because expected frequencies of two or more nights in the same shelter were very low, data for all classes > 1 were combined.

A χ^2 goodness of fit test showed that observed and expected frequencies differed significantly ($\chi^2 = 155.0$ 1 df, $P < 0.0001$, Table 7.3.). Toads returned to the same shelter on two or more consecutive samples 39% of the time, but were only expected to at a rate of 5%.

Table 7.3. Number of consecutive nights that toads used the same shelter and expected number based on Monte Carlo simulation of random shelter selection.

Number of Consecutive Nights	Observed Frequency (%)	Expected Frequency
1	177 (59.4)	281.58
2	59 (19.8)	14.63
3	35 (11.7)	0.75
4	14 (4.7)	0.038
5	6 (2.0)	0.002
>5	7 (2.3)	0.0001

7.3.7 Toad Length and Body Condition.

The snout-vent length (SVL) and the body mass of the toads at the initial introduction were compared to that of the same toads ($n = 36$) towards the end of the experiment (after sample 12). A paired t test performed on these data demonstrated a significant result in both length ($T = -7.27$, 35 d.f., $P < 0.001$) and weight ($T = 12.02$, 35 d.f., $P < 0.001$). During the course of this experiment there was an increase in SVL of the toads within the enclosure (before sample 1: $\bar{x} = 101.5$mm ± 1.21 S.E.; after sample 12: $\bar{x} = 105.1$mm ± 1.33 S.E.). Toad weight however, decreased (before sample 1: $\bar{x} = 94.08$g ± 3.63 S.E.; after sample 12: $\bar{x} = 84.92$ ± 3.99 S.E.). The loss of body weight may indicate dehydration of toads; the final weights were taken following an unwatered period.

7.4 Discussion.

7.4.1 Use of Cavities as Retreat Sites.

The use of daytime retreats allows toads to mitigate the effects of environmental stresses (van Gelder *et al.* 1986) and to avoid predation (Denton and Beebee 1993b). Field data suggest that limited availability of moist, sheltered retreat sites may be a major cause of mortality (Zug and Zug 1979). For toads in the Australian tropics during the dry season, the stresses of low water availability and high insolation can be reduced by the use of good daytime retreat sites.

Many toads did not use the artificial shelters during the initial samples (treatment U1). In these samples, 7% of toads were found in the pool of water, while 10% were discovered partially concealed in shallow depressions in the long grass. These depressions were similar to the "forms" described by Dole (1965). By the second set of three samples (treatment W), most toads were using the available artificial shelters (Table 7.1). This suggests that toads required an initial period of exploration, as found by Smits (1984), who concluded that *B. boreas* established a pattern of surface activity within a few days. It is also possible that the attractiveness of the artificial shelters increased as general moisture levels in the pen declined following the rainfall between samples 1 and 2.

7.4.2 Shelter Site Use and Soil Moisture.

Water loss of toads under the artificial shelters probably decreased by the enclosed nature of the shelters. Sheltering in cavities reduces air circulation (Dole 1965), increases ambient humidity levels (Pearson 1955), and reduces heat gain from insolation. Water loss in typical amphibians varies inversely with relative humidity (Wygoda and Williams 1991),

so burrows or other cavities are favourable microhabitats in which to maintain or restore a positive water balance (Smits 1984; Dobkin *et al.* 1989; Denton and Beebee 1993b). It is likely that the reduced insolation and air circulation under the artificial shelters in this study caused soil moisture levels to remain higher for longer periods than in the surrounding soil. Toads under artificial shelters would thus have experienced lower rates of desiccation and lower heat loading than toads using other retreat sites.

The distribution of toads within the enclosure was clearly related to soil moisture. Toads shifted to the half of the enclosure with the highest relative soil moisture. Similar effects occur in other species; Dole (1965) demonstrated that *Rana pipiens* retreat from dry areas to more suitable areas within a few days, and Blair (1960) stated that an increase in ground moisture increases the number of potential retreat sites. Toads may also move longer distances in response to lack of moisture; Carpenter and Gillingham (1987) suggested that *B. marinus* shifted from a dried-up waterhole to locate another site.

7.4.3 Effects of Temperature.

In addition to reducing their effective surface area/volume ratio and selecting retreat sites with higher humidity, toads can conserve water by selecting retreat sites with lower ambient temperatures (Malvin and Wood 1991). This benefit of reduced temperature is opposed by the need for elevated temperatures to facilitate digestion and nutrient absorption (Hoffman and Katz 1989; Huey *et al.* 1989; Preest and Pough 1989; Tracy *et al.* 1993). These tradeoffs appeared to affect the behaviour of toads in our experiment; they occurred more often under shelters with higher temperatures only when soil moistures were above zero.

7.4.4 Aggregation and Site Fidelity.

Toads aggregate at wintering sites (Tester and Breckenridge 1964). Harlequin frogs, *Atelopus varius*, aggregate in moist areas as the dry season progresses (Crump and Pounds 1989). Individuals of *B. marinus* formed closely packed aggregations under the artificial shelters in this experiment. Toads under the shelters adopted the typical water-conserving posture (Zug and Zug 1979). Tight packing of individuals in retreat sites should further reduce effective surface area/volume ratios and thus evaporative water loss. This type of behaviour is common in the field. I have found large aggregations of toads under tree roots, in hollow logs or under pieces of debris, such as bark and leaves, on river banks.

An additional advantage to aggregation may result from modifications toads make to their retreat sites. Toads often enter these sites with a full bladder. Toads appeared to frequently void their bladders under shelters, before they were disturbed. Transport of water by this means increases the moisture in the soil and in the surrounding air. Both the individuals transporting water and individuals who do not contribute to water transport may benefit from this.

This experiment demonstrated that toads have some degree of fidelity to retreat sites; toads returned to the same shelter much more often than they would have by chance (Table 7.3). Homing is common in anurans (Brattstrom 1962; Sinsch 1991). In the field toads may respond to dry weather by remaining in retreat sites (Stille 1952; Dobkin *et al.* 1989). Although toads in this experiment were displaced every two days, they often returned to their favoured shelter site. Similar results were found by Dole (1968) with *Rana pipiens*. These frogs demonstrated a high degree of precision when relocating home areas after being displaced moderate distances, some returning to their retreat sites up to eight days in a row. If toads regularly "invest" in retreat sites by voiding their bladders,

thus increasing soil moisture and humidity, this may increase the advantages of retreat-site fidelity.

7.5 Summary.

B. marinus clearly favoured areas and shelters that had moist soil. When soil moisture was elevated, they favoured shelters with higher soil temperatures. Toads often aggregated under shelters during this experiment. This behaviour may result in part from individuals selecting shelters with moist substrates independently of one another, and may also result from direct advantages of aggregation, such as reducing the effective surface area/volume ratio of individuals. Aggregation may also be favoured as a way of taking advantage of water transported in the bladders of other individuals and excreted in the shelter site. Once a favourable shelter was located, toads returned to it repeatedly. Toads shifted from their home shelters more frequently when conditions at the site became unfavourable: ie. too dry. A new shelter site with more favourable conditions was then selected. Field data (personal observation) suggests that shelter sites with good combinations of thermal and hydric characteristics that are close enough to water for regular rehydration may be a limiting resource for *B. marinus* during the dry season.

Chapter 8. Conclusion.

8.1 Seasonal Effects on Toads.

This thesis has examined ecological characteristics of two populations of the cane toad, *Bufo marinus*, in the seasonal wet-dry tropics of northern Australia. In general, ecological aspects of these populations are influenced by long, dry periods characterised by virtually no rainfall, low humidity and relatively high temperatures (ie. the dry season), and short wet periods of high rainfall and humidity and extreme temperatures (ie. the wet season) (Oliver 1978). The pattern of wet and dry seasons strongly affects the reproduction and demography of anurans (Gallati 1992) and *B. marinus* populations have survived and flourished in the wet-dry tropics of northern Australia for over 60 years (Alford *et al.* 1995). Toad populations therefore demonstrate ecological strategies that best allow them to cope with, and survive through, the dry season and maximise essential functions (ie. feeding and breeding) during the wet season.

The existence of seasonal patterns in abundance in tropical organisms and the influence of climatological factors has been well established (Wolda 1989). However, the causes of these patterns is less well documented. The majority of ecological characteristics of the two toad populations examined during this study are primarily determined and influenced by seasonal environmental factors such as rainfall, hydric requirements and temperature. These environmental factors influence difference aspects and life-stages of many amphibian species (Hemelaar 1988) including *B. marinus* populations. As for most amphibian species, *B. marinus* face a series of challenges to their growth and survival associated with the abiotic and biotic environment once tadpoles metamorphose and first emerge onto land (Semilitsch and Wilbur 1988; Pechmann *et al.* 1989; Berven 1990). Newly emerged metamorphs for example, remain close to the water's edge (see Chapter

3) suggesting that they actively avoid dessication due to the high temperatures experienced during the wet season (Freeland and Kerin 1991; Chapter 3).

Even when newly emerged metamorphs remain close to the water's edge their survival is still decreased by high temperatures. Smaller toads are less able to cope with hydric stresses associated with increased temperatures and are therefore under severe pressure to either grow rapidly and better cope with environmental stresses, or perish (Richards and Lehman 1980).

Small metamorphs at the edge of a waterbody also face challenges other than extreme environmental conditions. As most breeding activity of *B. marinus* occurs during a short period in the wet season (Chapter 5), and tadpole development at this time is relatively constant (Hearnden 1991), large numbers of toad metamorphs usually emerge from water at approximately the same time (ie. late in the wet season and at the commencement of the dry season). The density of metamorphs at the water's edge at this time is usually exceptionally high. Crowding and aggregation of metamorphs makes survival (Figure 3.2) and rapid growth (Figure 3.3) difficult (Pearson 1955; 1957). High densities of metamorphs led to lower growth rates and therefore prolonged their time as metamorphs thus exposing them to greater cummulative risks (Chapter 3).

It is clear that eggs laid early in the wet season by toads may develop quickly and with reduced competition (Hearnden 1991) and therefore emerge from water as metamorphs before the onset of the dry season. This provides small toads with better survival prospects into the dry through to the following wet season (Berven 1990).

The period of most risk for small newly emerged toads is probably only within the first three weeks of terrestrial life. After this time surviving metamorphs experience rapid growth rates that account for at least 80% of their adult size (Werner 1986) at

approximately 90mm snout-vent length (Figure 4.4; Zug and Zug 1979). During this period small toads may select environments that produce body temperatures that tend to minimise their rates of dehydration (Tracey *et al.* 1993). Nevertheless, high temperatures characteristic of the wet season initially increase toad mortality by dehydration. However, once small toads survive through the critical period immediately after their first emergence onto land, high temperatures may work in their favour , assuming high levels of food items are present, by increasing their growth rates (Chapter 4; Halliday and Verrell 1988).

Fast growth rates in amphibians, such as those shown by *B. marinus*, allow them to quickly pass through the stage with the greatest mortality (Chapman and Chapman 1958; Clarke 1974). Once a toad has attained a size of approximately 30mm many of the immediate problems experienced at the commencement of terrestrial life decrease. Although the responses of toads to environmental conditions are flexible and vary among individuals (Preest and Pough 1989), the survival of toads, especially juveniles, through the dry season to the following wet season is however, probably the greatest challenge toads face in the wet-dry tropics of northern Australia. The end of the wet season and commencement of a long dry period signals a major shift in toad activity. Breeding generally ceases (Hearnden 1991), and food supplies decrease (Jansen 1973) thus causing the rapid growth and higher body condition experienced by toads during the wet season to slow (Figures 4.5 and 4.6). The number of toads active alongside water courses at this time increased significantly (Figure 5.1) probably as a result of increasing hydric pressures placed on toads. Juvenile and sub-adult toads that first emerged onto land a few months earlier and have since spent time foraging away from water, now return to, and congregate in large numbers, at the water's edge.

After the transitional period between wet and dry season conditions become even drier and nocturnal temperatures decrease. Toad activity correspondingly declines significantly during the middle to late dry season and the requirement for a suitable shelter

site becomes essential for their continued survival. The quality and quantity of retreat sites are an essential resource for amphibian survival (Newman 1990; Ovaska 1991). Toads during this study were shown to select shelters with favourable hydric qualities (Figure 7.2) and return to suitable sites regularly (Table 7.3). The suitability of shelter sites has been shown to vary according to season (Schwarzkopf and Alford 1996), and toads aggregating in such shelters may further reduce hydric pressures (Section 7.4.4).

In addition to their choice of shelter sites, survival of toads through to the end of the dry season may depend on their body condition obtained prior to the onset of dry conditions (Chapman and Chapman 1958; Denton and Beebee 1993a). Toad body condition declines almost immediately after the wet season but increases quickly once conditions improve (Figure 6.3). Increasing nocturnal temperatures at the end of the dry season signal increased toad activity. As food supplies are low at this time (Galatti 1992), toad activity is probably a response to increasing hydric pressures.

The low proportion of sub-adult and juvenile toads within the population at the end of the dry season indicates that mortality of these age classes through the dry season is high. Furthermore, surviving non-adult toads demonstrated the lowest body condition indicated that a failed wet season would almost certainly lead to their mortality. Similar results were demonstrated by Ovaska (1991) and Berven (1990). This decline in the activity estimates of non-adult toads was especially evident at Townsville sites during the latter part of the study due to poor wet season rains.

If toads can survive through the dry season into the following wet season then they have the opportunity to rapidly increase their body condition, undergo rapid growth and breed successfully. Once wet season rains commence toad activity undergoes a change. Female toads and some males move away from water courses where they can successfully forage and maintain their hydric requirements. This pattern of activity has been previously

shown for *B. marinus* by Carpenter and Gillingham (1987). However, their study also concluded that toads returned to permanent water sources to breed or to rehydrate during dry periods. Crump and Pounds (1989) and Chapman and Chapman (1958) also showed that frogs will generally congregate at water sources during dry periods. Fluctuations in toad activity during this period are probably accounted for by changing climatic conditions. For example, after recent rainfall toads dispersed away from water but their presence at a watercourse increased with time since a previous rainfall event (Table 5.3).

As with other anuran species, once adult size is attained by *B. marinus*, rapid rate of growth generally ceases and they probably undergo a resource allocation shift from somatic growth to reproduction (Halliday and Verrell 1988). The main breeding season of anurans in tropical regions corresponds to the height of the wet season rains (Jørgensen *et al* 1986) In the wet-dry tropics of northern Australia *B. marinus* also follows this seasonal pattern of breeding (Freeland 1984).

Although primarily covered by Hearnden (1991), some conclusions about breeding ecology of *B. marinus* can be drawn. For example, male *B. marinus*, as with most amphibian species, maximise their breeding potential by regularly being active around a watercourses during the wet season (Aichinger 1987). Females, on the other hand, will only come down to the water's edge when they are ready to breed or hydric requirements are paramount (Hearnden 1991). This variation in activity patterns between the sexes led to a male-biased sex ratio especially during the height of the wet season (Figure 5.3a). A male-biased sex ratio has been previously noted for several anuran species (eg. Christein and Taylor 1978; Gittens *et al.* 1980; Gittens 1983; Breden 1988 and Berven 1990).

As expected during the wet season a higher proportion of large, potentially breeding male and female toads were present along watercourses. During this time individual adult size was generally larger (Figure 5.4a and b). The larger size of female toads recorded

during the study is probably related to fecundity and a greater reproductive effort (Gibbons and McCarthy 1984) with a larger body size producing more numerous and larger egg masses (Tejedo 1992b) which may lead to an increased breeding potential (Hemelaar 1988). Larger body size in male toads during the breeding season may also be an advantage by displacing or out competing smaller males during amplexus (Hillis *et al.* 1984) therefore providing more input into toad populations with a single peak or continuous breeding activity (Tejedo 1992a) such as *B. marinus.*

8.2 Variations Between Locations.

Although both Calvert Hills and Townsville are situated in the wet-dry tropics of northern Australia, *B. marinus* populations showed considerable variation between locations. Climatic variation between the two regions, such as differences in the length and amount of rain during the wet and dry seasons, influenced several aspects of the ecology of *B. marinus*.

The harsher climatic conditions experienced at Calvert Hills, such as a longer and hotter dry season and shorter duration and intensity wet season, caused a reduction in the length of toad breeding behaviour, increased hydric stresses, and higher rates of growth and mortality. Toad populations at Calvert Hills must breed quicker than those at Townsville because of a shorter duration wet season. Furthermore, new generations demonstrated a rapid increase in energy stores and growth rates during favourable conditions. A faster attainment of reproductive status may enhance survival of toads at this location by best coping with harsh environmental influences (Ryser 1988). When conditions become unfavourable (ie. the onset of the dry season), characterised by high diurnal temperatures and associated hydric stresses and reduced food availability, toads must be in good condition and utilise their energy stores if they are to survive through to the following wet

season. The selection of suitable refuge sites is therefore imperative for toads at Calvert Hills during the dry season to reduce desiccation risks during periods of inactivity.

In contrast to Calvert Hills, the climate of the Townsville region is less harsh with lower temperatures, a longer and usually more intense period of rain during the wet season and more dry season rainfall. Environmental factors at Townsville may not influence ecological aspects of toad populations to the extent of those experienced at Calvert Hills. Other abiotic factors, such as site variations and competition pressures, may therefore be more influential on toad growth rates, body condition and seasonal changes in body size of Townsville populations.

Activity patterns of male toads at Townsville also contrasted those recorded at Calvert Hills. Male toads at Townsville congregated around water courses over a longer period of time including much of the wet season. This aggregation behaviour probably allows male toads a higher breeding potential when females decide to come down to the water's edge to breed (Tejedo 1992a).

8.3 Implications for Biocontrol.

Since its introduction into Australia in 1935 the cane toad, *B. marinus*, has successfully colonised large areas of Australia including the east coast from Cape York in the north and northern New South Wales to the south. In addition, the toad is currently expanding its range westward into the Northern Territory at a rapid rate and is likely to colonise large areas of Arnhem Land and Kakadu National Park early next century (Freeland and Martin 1985). The presence of toads in the Australian environment is considered to be detrimental to many native fauna species and a biocontrol program is therefore desirable (Freeland 1985; Alford *et al.* 1995). This study examined several

aspects of *B. marinus* population ecology that may provide useful baseline data for possible future biocontrol of the species.

A successful biocontrol agent on the terrestrial stage of *B. marinus* should be targeted where it will be most effective, ie. when populations and/or particular age categories are under extreme survival pressures. This study has demonstrated that *B. marinus* populations are under extreme hydric stress during the dry season in the wet-dry tropics of Northern Australia. This is especially evident towards the end of the dry season when surviving toads must actively rehydrate (due to the increasing temperatures), have a low body condition and probably experience a high rate of natural mortality. However, if toads survive until the early phase of the wet season they have the opportunity to rapidly improve their body condition due to increasing food resources and successfully breed the next generation of toads.

The advantages of implementing a biocontrol agent late in the dry season are therefore:

a. toads are easy to locate as their activity patterns during this period are relatively high and usually associated with water; and

b. toad populations are probably under extreme stress after surviving a long dry period with little or no food in an extremely dehydrating environment.

The vulnerability of toads when they first emerge onto land at approximately 8mm in length through to juvenile size (approximately 30mm) has also been identified during this study as a period when toad survival is under severe stress. Very high densities of newly emerged toads crowd at the water's edge while they undergo postmetamorphic physiological changes (Pough and Kamel 1984). It is during this period when metamorphs

experience very high rates of mortality (Licht 1974; Freeland and Kerin 1991) due to the harsh physical environment, predators and competition (Chapter 3). The advantage of using a biocontrol agent during this life history phase is that the majority of individuals are concentrated within the first few metres of the water's edge. However, this life-history stage already has a high rate of natural mortality and combined with large numbers of metamorphs emerging from water sources this period of the terrestrial stage of *B. marinus* is probably unsuitable for biocontrol methods.

Having now isolated areas of the ecology of the terrestrial stages of the life-history of *B. marinus* that are most vulnerable, the challenge is now for scientists involved with biological control to find an agent that can exploit these areas of weakness.

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Appendices.

Appendix 1. Time of year and season for sampling trips to Calvert Hills including number of samples at Big Calvert River (BCR) and Homestead (HOM) sites. (One sample equals a one night census of mark-recapture).

Trip Number	Months/Year	Season	Number of Samples	
			BCR	HOM
1	Nov/Dec 1986	Early-wet	3	3
2	May 1987	Late-wet/early-dry	3	3
3	Sept 1987	Late-dry	2	2
4	Jan 1988	Middle-wet	2	2
5	Feb 1988	Late-wet/early-dry	2	2
6	Apr/May 1988	Late-wet/early-dry	3	3
7	Aug 1988	Late-dry	3	3
8	Jan/Feb 1989	Middle-wet	3	3
9	Jun 1989	Middle-dry	3	3
10	Apr 1991	Late-wet/early-dry	3	3
11	Nov/Dec 1991	Early-wet	3	3
12	Apr 1992	Late-wet/early-dry	3	3

Appendix 2. Time of year and season for sampling trips at Townsville sites including the number of samples at Bentley Lagoon (BEN), Rock's Road (ROX) and Bell's Dam (BEL). (One sample equals a one night census of mark-recapture).

Trip Number	Months/Year	Season	Number of Samples		
			BEN	ROX	BEL
1	Nov/Dec 1986	Early-wet	3	3	3
2	Apr 1987	Late-wet/Early-dry	1	1	1
3	May/Jun 1987	Middle-dry	3	3	3
4	Sep/Oct 1987	Late-dry	2	1	2
5	Nov 1987	Early-wet	1	1	1
6	Mar/Apr 1988	Middle-wet	3	3	3
7	Aug 1988	Middle-dry	1	1	1
8	Oct 1988	Late-dry	1	1	1
9	Jan 1989	Middle-wet	1	1	1
10	Mar 1989	Middle-wet	1	1	1
11	May/Jun 1989	Late-wet/Early-dry	1	1	1
12	Sep 1989	Late-dry	3	3	3
13	Oct 1989	Late-dry	3	3	3
14	Mar/Apr 1991	Late-wet/Early-dry	3	3	3
15	Jun/Jul 1991	Late-dry	3	3	3
16	Oct/Nov 1991	Late-dry	2	3	2
17	Mar 1992	Late-wet/Early-dry	3	3	3
18	Jul/Aug 1992	Middle-dry	3	2	0
19	Aug 1992	Late-dry	1	1	0
20	Nov/Dec 1992	Early-wet	2	2	0
21	Dec 1992	Middle-wet	1	1	0
22	Jan 1993	Middle-wet	3	3	0

Appendix 3. Rainfall records (mm) during study period (1986-1993) for Calvert Hills, Wollogorang Station and Townsville. (* = no record).

Month	Calvert Hills							
	1986	1987	1988	1989	1990	1991	1992	1993
January	38.8	248.2	55.2	135.6	*	301.4	75.1	*
February	19.8	463.2	48.6	0	*	201.8	108.3	*
March	39.2	9.8	71.2	327.6	*	0	39.7	*
April	2	0	35	16.8	*	0.2	1.8	*
May	18.8	1.5	4	*	*	0	50.4	*
June	0.8	6.4	0	*	*	4.5	*	*
July	47.4	0	0	*	*	0	*	*
August	0	0	0	*	*	0	*	*
September	6.8	0.2	0	*	*	0	*	*
October	69.6	0.8	0	*	*	0	*	*
November	18	165.9	9	*	*	48	*	*
December	66	96.9	235.7	*	*	40.2	*	*
Wollogorang								
January	*	122	88.7	203.6	70.4	*	*	*
February	*	*	114	104.4	100.6	*	*	*
March	*	*	176.4	466.8	0	*	*	*
April	*	18	19.4	32.6	29.2	*	*	*
May	*	1.2	1	1.8	8.2	*	*	*
June	*	19.8	0	15.6	4.6	*	*	*
July	33	0	0	0	*	*	*	*
August	8.2	0	1.8	0	*	*	*	*
September	1.2	14.6	1.6	0	*	*	*	*
October	24.7	1.6	1	8	*	*	*	*
November	64.8	49.2	63	66.8	*	*	*	*
December	56.9	132.7	307.6	57.1	*	*	*	*

Appendix 3. (Cont.).

Month	Townsville							
	1986	1987	1988	1989	1990	1991	1992	1993
January	254.6	216.2	14.6	56.6	27.2	458.2	27	66.2
February	113.8	85.6	208.4	146.4	8	865.4	227.8	109.2
March	29.6	47.2	10	311.4	682.8	14.8	7.2	36.6
April	27.8	6.6	65.6	172	406.4	1.2	5.4	8.2
May	52.4	15.2	13.2	138.4	53	17.2	54.6	13.8
June	1.4	13.2	1	36	96.6	9.6	6.6	3.2
July	2.4	9.8	43	30.6	12.8	0.6	1.8	*
August	26.4	6.6	4.8	8.8	0	0	1.8	*
September	37.8	1.8	0	0.2	0.6	0	33.2	*
October	26.4	18.6	6.6	16.2	2.4	3.2	3.8	*
November	26.4	56.6	87.8	100.8	0.2	21.2	49.4	*
December	25	290.2	355.6	104.4	377.8	138.8	179.2	*

Appendix 4. Summary of unweighted least squares linear regression of specific growth rate (SGR) for toads at Calvert Hills and Townsville.

	Coefficent	SE	N	$T_{0.05}$	Confidence Limits
Recipical Length					
Calvert Hills	0.51377	0.03465	80	2.96	0.4112 - 0.6163
Townsville	0.22931	0.02016	249	2.96	0.1696 - 0.2890
Constant					
Calvert Hills	-0.0041	3.942×10^{-4}	80	2.96	-5.28×10^{-3} - -2.94×10^{-3}
Townsville	-0.0018	2.081×10^{-4}	249	2.96	-2.02×10^{-3} - -1.60×10^{-3}

Appendix 5. ANOVA with Sites Separate.

There was a significant variation in toad numbers in all age categories at both locations (Table 6.1) (Calvert Hills: 3 df, F = 5.54, *P* = 0.0011; Townsville: 3 df, F = 30.44, *P* = 0.0001). Season by age category effects on toad densities at both localities were also significant (Calvert Hills: 12 df, F = 3.81, *P* = 0.0001; Townsville: 12 df, F = 2.13, *P* = 0.0121). Calvert Hills toad densities were also significantly effected by season (4 df, F = 26.69, *P* = 0.0001), while no seasonal effect was demonstrated on Townsville toad densities.

Summary of the results of 3-way ANOVA on toad densities at Calvert Hills and Townsville. (* = significant at 0.05 level).

	Calvert Hills				Townsville			
	d.f.	**MS**	**F**	***P***	**d.f.**	**MS**	**F**	***P***
Site	1	107.58	0.27	0.6005	2	1910.53	1.68	0.1223
Season	4	10441.2	26.7	0.0001*	4	1853.82	2.59	0.087
Age Category	3	2168.97	5.54	0.0011*	3	28035.6	30.4	0.0001*
Site*Season	4	417.65	1.07	0.3734	8	1199.15	1.49	0.2288
Site*Age Category	3	247.53	0.63	0.5947	6	672.13	0.83	0.6154
Season*Age Category	12	1491.58	3.81	0.0001*	12	1967.56	2.13	0.0121*
Site*Season*Age Category	12	193.99	0.5	0.916	24	410.38	0.53	0.9888
Error (Residual)	224	391.26	-	-	428	904.83	-	-

Appendix 6. Environmental variables measured during study for Calvert Hills sites, Big Calvert River and Homestead. Temperatures are in ° C, while cloud cover and humidity are percentages. (* = no record).

Big Calvert River

Date	Season	Air Temp.	Soil Temp.	Humidity	Cloud Cover
25.11.86	Early-wet	*	*	*	*
27.11.86	Early-wet	*	*	*	*
29.11.86	Early-wet	*	*	*	*
5.5.87	Late-wet/Early-dry	29	30	46	0
7.5.87	Late-wet/Early-dry	26	27	78	50
9.5.87	Late-wet/Early-dry	28	30	62	0
2.9.87	Late-dry	21	12	46	0
5.9.87	Late-dry	24	15	77	0
17.1.88	Middle-wet	30	32.5	89	0
19.1.88	Middle-wet	28	34	85	0
2.2.88	Late-wet/Early-dry	*	32.5	*	25
8.2.88	Late-wet/Early-dry	22	28	92	0
6.5.88	Late-wet/Early-dry	*	32	*	0
12.5.88	Late-wet/Early-dry	24.5	*	57	0
17.5.88	Late-wet/Early-dry	24.5	28.5	92	100
10.8.88	Late-dry	19	20	46	0
15.8.88	Late-dry	25	23.5	70	25
21.8.88	Late-dry	26.5	25.5	68	0
3.2.89	Middle-wet	*	30.5	*	0
5.2.89	Middle-wet	31	35	67	25
7.2.89	Middle-wet	27	34.5	85	25
15.6.89	Middle-dry	17	23	90	0
18.6.89	Middle-dry	19.5	23	74	0
20.6.89	Middle-dry	15.5	18.5	50	0
22.4.91	Late-wet/Early-dry	22.5	24.5	92	100
25.4.91	Late-wet/Early-dry	25	27	81	0
27.4.91	Late-wet/Early-dry	16	24	76	0
29.11.91	Early-wet	25	28	84	25
30.11.91	Early-wet	26	27.5	85	0
3.12.91	Early-wet	29.5	29	73	0
20.4.92	Late-wet/Early-dry	26	31	85	0
22.4.92	Late-wet/Early-dry	27	29	71	0
24.4.92	Late-wet/Early-dry	25.5	29.5	67	0

Appendix 6. (Cont.)

Homestead

Date	Season	Air Temp.	Soil Temp.	Humidity	Cloud Cover
2.12.86	Early-wet	27.5	*	*	*
4.12.86	Early-wet	27.5	*	*	*
6.12.86	Early-wet	26.5	*	*	*
11.5.87	Late-wet/Early-dry	25	29	72	0
12.5.87	Late-wet/Early-dry	27.5	30	75	25
13.5.87	Late-wet/Early-dry	27.5	30	75	0
4.9.87	Late-dry	23.5	15	62	0
7.9.87	Late-dry	25.5	18	55	75
14.1.88	Middle-wet	26.5	29	85	0
20.1.88	Middle-wet	27	29.5	78	75
6.2.88	Late-wet/Early-dry	26.5	28	92	75
10.2.88	Late-wet/Early-dry	*	*	*	100
23.4.88	Late-wet/Early-dry	24.5	*	74	0
10.5.88	Late-wet/Early-dry	27	*	41	0
15.5.88	Late-wet/Early-dry	25	25.5	77	0
13.8.88	Late-dry	24.5	22	63	0
17.8.88	Late-dry	25	25.5	70	0
23.8.88	Late-dry	23	20	45	0
30.1.89	Middle-wet	23.5	27	96	100
31.1.89	Middle-wet	26	28	88	100
1.2.89	Middle-wet	29	27.5	76	50
16.6.89	Middle-dry	18.5	22	82	0
19.6.89	Middle-dry	16	18.5	54	0
21.6.89	Middle-dry	14	17.5	65	0
23.4.91	Late-wet/Early-dry	24	25	84	25
26.4.91	Late-wet/Early-dry	21	24	75	0
29.4.91	Late-wet/Early-dry	19.5	23	74	0
30.11.91	Early-wet	28.5	30	66	0
3.12.91	Early-wet	27.5	31.5	79	0
5.12.91	Early-wet	32	35	65	25
21.4.92	Late-wet/Early-dry	27.5	29	56	25
23.4.92	Late-wet/Early-dry	27.5	31	65	25
25.4.92	Late-wet/Early-dry	27	29	30	0

Appendix 7. Environmental variables measured during study for Townsville sites, Bentley Lagoon, Rock Road Dam and Bell's Dam. Temperatures are in °C, while cloud cover and humidity are percentages. (* = no record).

Bentley Lagoon

Date	Season	Air Temp.	Soil Temp. (10m)	Humidity	Cloud Cover
5.11.86	Early-wet	23	*	*	100
13.11.86	Early-wet	25	*	*	25
18.12.86	Early-wet	27.5	*	*	25
27.4.87	Late-wet/Early-dry	25	26.5	81	0
24.5.87	Middle-dry	24	24	77	0
27.5.87	Middle-dry	23.5	23	80	0
31.5.87	Middle-dry	22	22	72	0
24.9.87	Late-dry	22	19	76	0
27.10.87	Late-dry	26.5	22	89	25
23.11.87	Late-dry	27.5	*	79	0
27.3.88	Middle-wet	24.5	25	74	25
4.4.88	Middle-wet	23	28	84	0
12.4.88	Middle-wet	19.5	24	66	0
1.8.88	Middle-dry	22	21	72	100
18.10.88	Late-dry	24	29	92	25
23.1.89	Middle-wet	*	*	*	0
19.3.89	Middle-wet	25.5	27	92	50
28.5.89	Late-wet/Early-dry	21	22	87	25
12.9.89	Late-dry	14.5	19	90	0
13.9.89	Late-dry	18.5	19	74	0
14.9.89	Late-dry	19	21	82	25
17.10.89	Late-dry	25	25	81	0
18.10.89	Late-dry	22	24	87	0
19.10.89	Late-dry	22	24	79	0
19.3.91	Late-wet/Early-dry	21	26	96	0
26.3.91	Late-wet/Early-dry	25.5	27	92	0
3.4.91	Late-wet/Early-dry	25	27	84	0
17.6.91	Late-dry	17.5	21	95	0
23.6.91	Late-dry	20	21.5	83	0
2.7.91	Late-dry	19.5	*	91	0
29.10.91	Late-dry	25	26	84	25
30.10.91	Late-dry	25	24	74	0
6.3.92	Late-wet/Early-dry	27	30	78	0
13.3.92	Late-wet/Early-dry	28	31	79	25
20.3.92	Late-wet/Early-dry	25.5	27	78	25
29.7.92	Middle-dry	*	*	*	0
5.8.92	Middle-dry	21.5	23	72	0
9.8.92	Middle-dry	23	*	76	0
17.8.92	Late-dry	19	23	91	0
30.11.92	Early-wet	28.5	32	72	0
2.12.92	Early-wet	27	31	75	0
17.12.92	Middle-wet	26	27	74	25
22.1.93	Middle-wet	27	31	92	25
23.1.93	Middle-wet	26	29	85	0
25.1.93	Middle-wet	26	28	88	0

Rock Road Dam

Date	Season	Air Temp.	Soil Temp. (10m)	Humidity	Cloud Cover
3.11.86	Early-wet	22	*	*	0
10.11.86	Early-wet	21.5	*	*	0
16.12.86	Early-wet	26.5	*	*	25
23.4.87	Late-wet/Early-dry	24.5	24	67	25
25.5.87	Middle-dry	24	25	80	0
28.5.87	Middle-dry	17.5	21	69	0
1.6.87	Middle-dry	23	22	65	75
27.9.87	Late-dry	*	17	*	0
29.11.87	Late-dry	27.5	*	82	50
22.3.88	Middle-wet	26.5	26	65	0
28.3.88	Middle-wet	25	25	77	25
11.4.88	Middle-wet	21	24.5	87	0
2.8.88	Middle-dry	21.5	19.5	68	50
20.10.88	Late-dry	23	30	88	0
25.1.89	Middle-wet	24	*	96	75
16.3.89	Middle-wet	26	29	92	25
1.6.89	Late-wet/Early-dry	16.5	21	90	0
19.9.89	Late-dry	18	19.5	95	0
20.9.89	Late-dry	16.5	19.5	95	0
21.9.89	Late-dry	15	16.5	90	0
24.10.89	Late-dry	25	27	77	0
25.10.89	Late-dry	25	26	84	0
26.10.89	Late-dry	25.5	27	81	0
21.3.91	Late-wet/Early-dry	20	22	96	0
31.3.91	Late-wet/Early-dry	21.5	27	88	0
8.4.91	Late-wet/Early-dry	21	24.5	87	0
19.6.91	Late-dry	22	24	76	75
1.7.91	Late-dry	15.5	21	95	0
3.7.91	Late-dry	21	22	79	75
4.11.91	Late-dry	22	27	92	0
5.11.91	Late-dry	24.5	31	84	0
6.11.91	Late-dry	26	28	78	0
9.3.92	Late-wet/Early-dry	25	27	77	100
18.3.92	Late-wet/Early-dry	27	29	92	50
22.3.92	Late-wet/Early-dry	21.5	24	92	0
31.7.92	Middle-dry	18	22	91	0
7.8.92	Middle-dry	22.5	23	87	0
19.8.92	Middle-dry	22.5	26	72	25
1.12.92	Early-wet	28	31	79	25
3.12.92	Early-wet	27	31	85	100
16.12.92	Middle-wet	26	27	92	0
28.1.93	Middle-wet	27	27	78	25
29.1.93	Middle-wet	26	25.5	81	100
30.1.93	Middle-wet	25	26	77	50

Appendix 7. (Cont.).

Bell's Dam

Date	Season	Air Temp.	Soil Temp. (10m)	Humidity	Cloud Cover
7.11.86	Early-wet	25	*	*	0
14.11.86	Early-wet	*	*	*	0
19.12.86	Early-wet	28	*	*	0
22.4.87	Late-wet/Early-dry	22.5	24	100	75
26.5.87	Middle-dry	21.5	26	92	0
29.5.87	Middle-dry	16.5	21.5	59	0
2.6.87	Middle-dry	23.5	24	69	0
29.9.87	Late-dry	22.5	20	88	0
29.10.87	Late-dry	25.5	19	88	50
24.11.87	Late-dry	26.5	*	92	100
21.3.88	Middle-wet	26	27.5	92	50
29.3.88	Middle-wet	24	27.5	80	50
10.4.88	Middle-wet	24	26	73	0
3.8.88	Middle-dry	22.5	23	80	25
14.10.88	Late-dry	26	28	78	25
24.1.89	Middle-wet	24.5	*	92	75
15.3.89	Middle-wet	25.5	27.5	92	0
30.5.89	Late-wet/Early-dry	18	21.5	95	0
5.9.89	Late-dry	16	*	90	0
6.9.89	Late-dry	16	*	81	0
7.9.89	Late-dry	16	*	81	0
3.10.89	Late-dry	20	22	91	0
4.10.89	Late-dry	21	23	83	0
5.10.89	Late-dry	19.5	22	91	0
20.3.91	Late-wet/Early-dry	21.5	28	96	0
29.3.91	Late-wet/Early-dry	23	27	92	0
4.4.91	Late-wet/Early-dry	25	27	74	25
18.6.91	Late-dry	17.5	21.5	91	0
1.7.91	Late-dry	18	19.5	77	0
3.7.91	Late-dry	20	23	87	50
7.3.92	Late-wet/Early-dry	22.5	30	74	25
14.3.92	Late-wet/Early-dry	27	32	82	0
21.3.92	Late-wet/Early-dry	22.5	27	84	0

Appendix 8. Rainfall variables (mm) measured during study for Calvert Hills sites, Big Calvert River and Homestead.

Big Calvert River

Date	Season	Prev. 1 Day	Prev. 3 Days	Prev. 7 Days	Prev. 30 Days	Prev. 60 Days	Prev. 90 Days	Follow.30 Days
25.11.86	Early-wet	0	0	3	11.2	80.6	87.4	71
27.11.86	Early-wet	0	7	7	18	87.6	94.4	66
29.11.86	Early-wet	0	0	7	18	87.6	94.4	66
5.5.87	Late-wet/Early-dry	0	0	0	0	1.4	451.8	1.5
7.5.87	Late-wet/Early-dry	1	1	1	1	2.4	439.2	0.5
9.5.87	Late-wet/Early-dry	0	1	1	1	2.4	439.2	0.5
2.9.87	Late-dry	0	0	0	0	0	6.4	0.2
5.9.87	Late-dry	0	0	0	0	0	6.4	0.2
17.1.88	Middle-wet	0	12.2	23.7	67.2	164.3	288.1	66.5
19.1.88	Middle-wet	0	0	16.5	67.2	164.3	288.1	66.5
2.2.88	Late-wet/Early-dry	12.5	13.5	20.5	66.7	159.2	249.5	36.1
8.2.88	Late-wet/Early-dry	0	12	28.5	82.7	175.2	264.3	20.1
6.5.88	Late-wet/Early-dry	0	0	0	11.4	106.2	126.3	4
12.5.88	Late-wet/Early-dry	0	0	0	11.4	106.2	118.8	4
17.5.88	Late-wet/Early-dry	2	2	2	13.4	108.2	120.8	2
10.8.88	Late-dry	0	0	0	0	0	4	0
15.8.88	Late-dry	0	0	0	0	0	2	0
21.8.88	Late-dry	0	0	0	0	0	0	0
3.2.89	Middle-wet	0	0	74	129.6	372	381	17
5.2.89	Middle-wet	0	0	74	129.6	372	381	102
7.2.89	Middle-wet	0	0	0	129.6	348.2	381	158
15.6.89	Middle-dry	0	0	0	17	17.4	148.4	0
18.6.89	Middle-dry	0	0	0	17	17.4	56	0
20.6.89	Middle-dry	0	0	0	17	17.4	56	0
22.4.91	Late-wet/Early-dry	0.2	0.2	0.2	0.2	20	202	0
25.4.91	Late-wet/Early-dry	0	0	0.2	0.2	0.2	202	0
27.4.91	Late-wet/Early-dry	0	0	0.2	0.2	0.2	202	0
29.11.91	Early-wet	0	4	13.7	48	48	48	40.2
30.11.91	Early-wet	0	0	13.7	48	48	48	40.2
3.12.91	Early-wet	0	0	4	48	48	48	70.6
20.4.92	Late-wet/Early-dry	0	0	0.5	11.1	97	168.2	50.4
22.4.92	Late-wet/Early-dry	0	0	0	11.1	94.6	168.2	50.4
24.4.92	Late-wet/Early-dry	0	0	0	11.1	89.7	158.2	50.4

Appendix 8. (Cont.)

Homestead

Date	Season	Prev. 1 Day	Prev. 3 Days	Prev. 7 Days	Prev. 30 Days	Prev. 60 Days	Prev. 90 Days	Follow. 30 Days
2.12.86	Early-wet	0	0	7	18	87.6	94.4	66
4.12.86	Early-wet	0	14	14	32	101.6	105.2	79
6.12.86	Early-wet	0	0	14	32	101.6	105.2	79
11.5.87	Late-wet/Early-dry	0	0	1	1	2.4	439.2	0.5
12.5.87	Late-wet/Early-dry	0	0	1	1	2.4	439.2	0.5
13.5.87	Late-wet/Early-dry	0	0	1	1	1	424.4	0.5
4.9.87	Late-dry	0	0	0	0	0	6.4	0.2
7.9.87	Late-dry	0	0	0	0	0	6.4	0.2
14.1.88	Middle-wet	4.3	11.5	11.5	99	193.1	276.1	78.7
20.1.88	Middle-wet	0	0	16.5	67.2	156.6	288.1	77.7
6.2.88	Late-wet/Early-dry	12	12	29.5	82.7	175.2	265.5	20.1
10.2.88	Late-wet/Early-dry	2.8	2.8	14.8	85.5	178	267.1	17.3
23.4.88	Late-wet/Early-dry	0	0	0	83.2	96.2	151.4	15.4
10.5.88	Late-wet/Early-dry	0	0	0	11.4	106.2	123.5	4
15.5.88	Late-wet/Early-dry	0	0	0	11.4	106.2	118.8	4
13.8.88	Late-dry	0	0	0	0	0	4	0
17.8.88	Late-dry	0	0	0	0	0	0	0
23.8.88	Late-dry	0	0	0	0	0	0	0
30.1.89	Middle-wet	52	52	52	113.6	350	359	22
31.1.89	Middle-wet	22	74	74	135.6	372	381	0
1.2.89	Middle-wet	0	0	74	129.6	372	381	17
16.6.89	Middle-dry	0	0	0	17	17.4	136.6	0
19.6.89	Middle-dry	0	0	0	17	17.4	56	0
21.6.89	Middle-dry	0	0	0	17	17.4	46.8	0
23.4.91	Late-wet/Early-dry	0	0.2	0.2	0.2	16.6	202	0
26.4.91	Late-wet/Early-dry	0	0	0.2	0.2	0.2	202	0
29.4.91	Late-wet/Early-dry	0	0	0	0.2	0.2	202	0
30.11.91	Early-wet	0	0	13.7	48	48	48	40.2
3.12.91	Early-wet	0	0	4	48	48	48	70.6
5.12.91	Early-wet	1.2	1.2	1.2	49.2	49.2	49.2	71.1
21.4.92	Late-wet/Early-dry	0	0	0	11.1	94.6	168.2	50.4
23.4.92	Late-wet/Early-dry	0	0	0	11.1	92	168.2	50.4
25.4.92	Late-wet/Early-dry	0	0	0	11.1	48.9	158.2	50.4

Appendix 9. Rainfall variables (mm) measured during study for Townsville sites, Bentley Lagoon, Rock Road Dam and Bell's Dam.

Bentley Lagoon

Date	Season	Prev. 1 Day	Prev. 3 Days	Prev. 7 Days	Prev. 30 Days	Prev. 60 Days	Prev. 90 Days	Follw. 30 Days
5.11.86	Early-wet	5.4	13.4	21	40.8	78.6	105	30.4
13.11.86	Early-wet	0	1.2	1.8	40.4	81.4	84	34.2
18.12.86	Early-wet	0	0	0	25	74.4	115.6	116.2
27.4.87	Late-wet/Early-dry	1	1	5.2	6.4	53.6	154.6	15.4
24.5.87	Middle-dry	0	0	0	16.4	22.6	69	11.2
27.5.87	Middle-dry	0	0	0	15.4	21.8	69	13.2
31.5.87	Middle-dry	0	0	0	15.2	21.8	66.2	13.2
24.9.87	Late-dry	0	0	0	1.8	18	18.2	14.2
27.10.87	Late-dry	0	0	1.6	14.2	16	22.6	49.8
23.11.87	Late-dry	0	0.2	11.2	49	63.2	65	55.8
27.3.88	Middle-wet	0	0	0	123.6	217	447	57.2
4.4.88	Middle-wet	5.6	7	7.4	10.6	222.2	239.6	68.4
12.4.88	Middle-wet	0	0	3.4	13	172.4	241.8	65
1.8.88	Middle-dry	0	0	0	42.4	44	47.2	4.8
18.10.88	Late-dry	0	0	0	0	4.2	4.8	27
23.1.89	Middle-wet	0	0	10.2	225	425.2	504	144.8
19.3.89	Middle-wet	44.8	47.6	81.6	149.4	293.8	528.4	288.4
28.5.89	Late-wet/Early-dry	0.2	59	102	138.4	342.6	621.8	33.2
12.9.89	Late-dry	0	0	0	8.8	14.8	42.6	0.2
13.9.89	Late-dry	0	0	0	8.8	14.8	42.6	0.2
14.9.89	Late-dry	0	0	0	8.8	8.8	42.6	0.4
17.10.89	Late-dry	0	0	0.2	0.4	9	9.2	32
18.10.89	Late-dry	0	0	0.2	0.4	9	9.2	32
19.10.89	Late-dry	0	0	0.2	0.4	9	9.2	32
19.3.91	Late-wet/Early-dry	0	0	1.8	368.8	917.8	1333	5.8
26.3.91	Late-wet/Early-dry	3.6	4.4	4.4	22.2	888.2	1337	2.6
3.4.91	Late-wet/Early-dry	0	0	0.6	7.8	850.4	1282	1.8
17.6.91	Late-dry	0	0	0	17	19.8	25.6	8.8
23.6.91	Late-dry	0	8.2	8.2	10	26.8	33	0.6
2.7.91	Late-dry	0	0	0	9.6	26.2	28	0.6
29.10.91	Late-dry	0.2	0.2	0.2	0.2	0.2	0.2	24.2
30.10.91	Late-dry	3	3.2	3.2	3.2	3.2	3.2	21.2
6.3.92	Late-wet/Early-dry	0	0	79.6	208.6	254.6	393.8	7.2
13.3.92	Late-wet/Early-dry	0	0	6.2	135.2	242.8	272.6	3.2
20.3.92	Late-wet/Early-dry	1	1	1	127.6	241.6	262	4.8
29.7.92	Middle-dry	0	0	0	1.8	8.4	63	1.8
5.8.92	Middle-dry	0	0	0	0	8.4	62	4
9.8.92	Middle-dry	0	0	1.8	1.8	3.6	60.4	4.2
17.8.92	Late-dry	0	0	0	1.8	3.6	12.4	33.2
30.11.92	Early-wet	0	0	12.4	49.4	53.2	86.4	179.2
2.12.92	Early-wet	0	0	0	48.4	53.2	86.2	179.2
17.12.92	Middle-wet	0.4	0.4	0.4	121.2	160	161.4	106.2
22.1.93	Middle-wet	0	0	7.4	42.4	228.8	268.2	137.8
23.1.93	Middle-wet	0	0	2	42.4	228.8	268.2	137.8
25.1.93	Middle-wet	0	0	0	39.6	216.4	268.2	137.8

Rock Road Dam

Date	Season	Prev. 1 Day	Prev. 3 Days	Prev. 7 Days	Prev. 30 Days	Prev. 60 Days	Prev. 90 Days	Follow. 30 Days
3.11.86	Early-wet	0	0	7.6	26.4	64.2	90.6	27.8
10.11.86	Early-wet	0	0.6	16	39.8	80.2	106.2	35.4
16.12.86	Early-wet	0	0	0	34.2	74.6	115.6	116.2
23.4.87	Late-wet/Early-dry	4.2	4.2	4.2	6.2	52.6	174.2	16.4
25.5.87	Middle-dry	0	0	0	16.4	22	69	13.2
28.5.87	Middle-dry	0	0	0	15.4	21.8	69	13.2
1.6.87	Middle-dry	0.4	0.4	0.4	13.8	22.2	63.6	12.8
27.9.87	Late-dry	0	0	0	1.8	8.4	18.2	14.2
29.11.87	Late-dry	0	11.2	12	57.4	75.2	77	142.4
22.3.88	Middle-wet	0	0	0.2	124	228.2	477.2	23.4
28.3.88	Middle-wet	2	2	2	125.6	219	380.6	55.2
11.4.88	Middle-wet	0	3.4	3.4	13	172.6	241.8	65
2.8.88	Middle-dry	0.6	0.6	0.6	43	44.6	47.8	4.2
20.10.88	Late-dry	0	0	0	0	4.2	4.8	27
25.1.89	Middle-wet	0	0	0	220.2	409.6	499.6	148.6
16.3.89	Middle-wet	0	24.2	36	101.8	256.4	480.8	336
1.6.89	Late-wet/Early-dry	0	0	59	138.4	300.2	621.8	36
19.9.89	Late-dry	0	0	0	8.6	8.8	42.2	0.4
20.9.89	Late-dry	0	0	0	8.6	8.8	42.2	0.4
21.9.89	Late-dry	0.2	0.2	0.2	8.8	9	42.4	0.2
24.10.89	Late-dry	1.2	3.4	3.4	3.6	12.4	12.6	44.6
25.10.89	Late-dry	0	3.4	3.4	3.6	12.4	12.6	47
26.10.89	Late-dry	0	1.2	3.4	3.6	12.4	12.6	107
21.3.91	Late-wet/Early-dry	0	0	0	123.8	884.8	1333	6.2
31.3.91	Late-wet/Early-dry	0.6	0.6	5.8	14.6	881	1338	1.2
8.4.91	Late-wet/Early-dry	0	0	0	7.6	576	1153	1.8
19.6.91	Late-dry	0	0	0	11	19.4	25.6	8.8
1.7.91	Late-dry	0	0	0	9.6	26.2	28	0.6
3.7.91	Late-dry	0	0	0	8.8	26.2	28	0.6
4.11.91	Late-dry	0	0	3.2	3.2	3.2	3.2	30.6
5.11.91	Late-dry	0	0	3	3.2	3.2	3.2	30.6
6.11.91	Late-dry	0	0	0	3.2	3.2	3.2	30.6
9.3.92	Late-wet/Early-dry	0.2	5	5	147	242	274.4	4.4
18.3.92	Late-wet/Early-dry	0	0	0	127.6	242.8	261	5.8
22.3.92	Late-wet/Early-dry	0	1	1	127.6	241.6	262	4.8
31.7.92	Middle-dry	0	0	0	1.8	8.4	63	1.8
7.8.92	Middle-dry	0	1.8	1.8	1.8	10.2	61.6	2.4
19.8.92	Middle-dry	0	0	0	1.8	3.6	12.2	33.2
1.12.92	Early-wet	0	0	12.4	48.4	53.2	86.4	179.2
3.12.92	Early-wet	0	0	0	48.4	53.2	84.2	182.2
16.12.92	Middle-wet	0	0	0	120.8	160	161	101.2
28.1.93	Middle-wet	0	6.8	6.8	44	223.2	275	131
29.1.93	Middle-wet	3.6	9	10.4	47.6	226.8	276.2	127.4
30.1.93	Middle-wet	18.6	22.2	29	66.2	245.4	293.8	108.8

Appendix 9. (Cont.).

Bell's Dam

Date	Season	Prev. 1 Day	Prev. 3 Days	Prev. 7 Days	Prev. 30 Days	Prev. 60 Days	Prev. 90 Days	Follow. 30 Days
7.11.86	Early-wet	0	6.4	15.4	41.8	79.6	106	35.6
14.11.86	Early-wet	0	1.2	1.8	40.4	81.4	84	34.2
19.12.86	Early-wet	0	0	0	2	74.4	115.6	180
22.4.87	Late-wet/Early-dry	0	0	0	2	48.4	170	20.6
26.5.87	Middle-dry	0	0	0	16.4	22	69	13.2
29.5.87	Middle-dry	0	0	0	15.4	21.8	69	13.2
2.6.87	Middle-dry	1.6	2	2	12.4	23.8	38.6	11.2
29.9.87	Late-dry	0	0	0	1.8	8.4	18.2	17.8
29.10.87	Late-dry	3.6	3.6	5.2	17.8	19.6	26.2	57.4
24.11.87	Late-dry	0	0	11.2	49	63.2	65	55.8
21.3.88	Middle-wet	0	0.2	0.2	124	228.2	477.2	13.6
29.3.88	Middle-wet	0	2	2	82.8	218.8	286.8	55.2
10.4.88	Middle-wet	0	3.4	9	13	181.2	241.8	65
3.8.88	Middle-dry	0	0.6	0.6	5.8	44.6	47.8	4.2
14.10.88	Late-dry	0	0	0	0	4.2	4.8	25.4
24.1.89	Middle-wet	0	0	10	225	425.2	499.6	144.8
15.3.89	Middle-wet	24.2	34	37.2	102.2	264	480.8	336
30.5.89	Late-wet/Early-dry	0	0.2	67	138.4	310.4	621.8	36
5.9.89	Late-dry	0	0	5.4	8.8	33	47.4	0.2
6.9.89	Late-dry	0	0	0	8.8	17	47.4	0.2
7.9.89	Late-dry	0	0	0	8.8	15	47.4	0.2
3.10.89	Late-dry	0	0	0	0.2	9	33.2	16.2
4.10.89	Late-dry	0	0	0	0.2	9	33.2	17
5.10.89	Late-dry	0	0	0	0.2	9	33.2	17
20.3.91	Late-wet/Early-dry	0	0	1.8	285.8	917.8	1333	5.8
29.3.91	Late-wet/Early-dry	0	0.8	5.2	15.8	887	1338	1.8
4.4.91	Late-wet/Early-dry	0	0	0.6	7.8	782.2	1240	1.8
18.6.91	Late-dry	0	0	0	17	19.8	25.6	8.8
1.7.91	Late-dry	0	0	0	9.6	26.2	28	0.6
3.7.91	Late-dry	0	0	0	8.8	26.2	28	0.6
7.3.92	Late-wet/Early-dry	0	0	0	172	254.6	383.8	9.4
14.3.92	Late-wet/Early-dry	0	0	6.2	135.2	242.8	272.6	3.6
21.3.92	Late-wet/Early-dry	0	1	1	127.6	241.6	262	4.8

Appendix 10. Maximum r-square multiple regression analysis results for measured environmental variables against the number of male, female, sub-adult and juvenile toads active at Calvert Hills.

Significant Variables	Parameter Estimate	F Value	Probability
Dependant Variable = Males (Intercept = -8.54)			
1) Rainfall Prev. 7-30 days	-0.71	45.35	0.0001
2) Rainfall Following 30 Days	0.41	34.67	0.0001
3) Rainfall Prev. 30-60 Days	0.15	22.06	0.0001
4) Rainfall Prev. 3-7 Days	-0.4	7.15	0.0103
5) Humidity %	0.31	6.95	0.0114
6) % Cloud Cover	-0.13	4.89	0.032
Dependant Variable = Females (Intercept = 7.03)			
1) Rainfall Prev. 7-30 Days	-0.4	79.42	0.0001
2) Rainfall Following 30 Days	0.23	59.43	0.0001
3) Rainfall Prev. 30-60 Days	0.07	32.02	0.0001
4) Rainfall Prev. 3-7 Days	-0.27	15.64	0.0003
Dependant Variable = Sub-adults (Intercept = 6.14)			
1) Rainfall Prev. 7-30 Days	-1	28.54	0.0001
2) Rainfall Following 30 Days	0.49	12.02	0.0012
3) Soil Temperature at 10m	2.7	9.02	0.0043
4) Rainfall Prev. 60-90 Days	0.06	6.76	0.0126
5) Rainfall Prev. 3-7 Days	-0.67	6.08	0.0176
6) Air Temperature°C	-2.06	4.95	0.0312
7) Rainfall Prev. 30-60 Days	0.12	4.5	0.0393
Dependant Variable = Juveniles (Intercept = 24.49)			
1) Rainfall Prev. 60-90 Days	0.15	21.8	0.0001
2) Rainfall Prev. 7-30 Days	-0.34	4.38	0.0414

Appendix 11. Maximum r-square multiple regression analysis results for measured environmental variables against the number of male, female, sub-adult and juvenile toads active at Townsville.

Significant Variables	Parameter Estimate	F Value	Probability
Dependant Variable = Males			
No Significant Variables			
Dependant Variable = Females (Intercept = 8.26)			
1) Rainfall Prev. 60-90 Days	0.04	11.77	0.0009
2) Rainfall Prev. 3-7 Days	-0.18	7.28	0.0083
3) Rainfall Prev. 30-60 Days	-0.02	7.08	0.0092
4) Rainfall Following 30 Days	-0.03	5.47	0.0214
5) Rainfall Prev. 7-30 Days	-0.03	5.46	0.0215
Dependant Variable = Sub-adults (Intercept = 7.67)			
1) Rainfall Prev. 60-90 Days	0.07	36.07	0.0001
2) Rainfall Prev. 7-30 Days	-0.08	8.22	0.0051
3) Rainfall Prev. 3-7 Days	-0.33	7.04	0.0093
Dependant Variable = Juveniles (Intercept = 28.84)			
1) % Cloud Cover	-0.36	9.68	0.0024
2) Rainfall Prev. 3-7 Days	-0.41	2.92	0.0905

Appendix 12. Maximum r-square multiple regression analysis results for body condition of adult male and female toads and rainfall variables at Calvert Hills and Townsville.

Significant Variables	Parameter Estimate	F Value	Probability
Dependant Variable = Body Condition of Calvert Hills Males (Intercept = 0.044)			
1) Average Rain per Day	2.95×10^{-5}	11.36	0.0008
2) Length of Rain Event	-5.88×10^{-6}	8.57	0.0035
3) Time Elapsed Since Event	-7.73×10^{-6}	47.9	0.0001
Dependant Variable = Body Condition of Calvert Hills Females (Intercept = 0.044)			
1) Time Since Elapsed Rain	-1.39×10^{-5}	60.64	0.0001
Dependant Variable = Body Condition of Townsville Males (Intercept = 0.044)			
1) Average Rain per Day	-6.76×10^{-5}	790.08	0.0001
2) Length of Rain Event	2.25×10^{-5}	453.71	0.0001
3) Time Elapsed Since Event	-7.99×10^{-6}	263.77	0.0001
Dependant Variable = Body Condition of Townsville Females (Intercept = 0.044)			
1) Average Rain per Day	-4.91×10^{-5}	68.09	0.0001
2) Length of Rain Event	4.51×10^{-5}	254.95	0.0001
3) Time Elapsed Since Event	-1.37×10^{-5}	136.59	0.0001